CATALOGUE

OF THE

FOSSIL CEPHALOPODA

IN THE

BRITISH MUSEUM
(NATURAL HISTORY)

PART V

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THE
AMMONOIDEA
OF THE
TRIAS (II)

BY
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PREFACE

THE first part of Dr. Spath's account of the Triassic Ammonoidea (Part IV of the 'Catalogue of Fossil Cephalopoda') appeared in 1934, and dealt with "the four super-families Pronoritida, Xenodiscida, Meekoceratida and Phylloceratida, as well as part of the Ceratitida, nearly all occurring in the Lower and Middle Trias"; the present part contains the remaining genera of the super-family Ceratitida and the rest of the families of the Middle and Upper Triassic. The circumstances of the time, however, and the desirability of avoiding undue delay in presenting to other workers the fruits of Dr. Spath's researches, have necessitated some restriction in the scope of this Part. The details of the species actually preserved in the Museum have been omitted, together with localized lists of the registered specimens. It was also reluctantly decided that illustrations could not be included in Part V, though it is certainly hoped that a separate volume of illustrations will be issued in due course. To give figures of one typical species of each genus and sub-genus, together with suture-lines, and in many cases thin sections of the inner whorls, would have been highly desirable but would have meant a very large number of text-figures and plates, and a considerable further delay. Some historical specimens, such as Salter's Himalayan ammonites, should certainly be refigured. In the case of the many types of St. Cassian species in the Klipstein Collection it would also be desirable to figure at least those referred to below as distinct forms, or as having been misinterpreted by previous authors. It may well be preferable, however, to refigure these small specimens at some future date when comparison can be made with larger, and in some cases better, material in the collections at Vienna and Munich.

In Part IV the student was referred to the extensive lists of literature in Diener (1915) and Kutassy (1933), but since these catalogues are not always easily accessible, while much literature has been added subsequently, a comprehensive bibliography to Parts IV and V has been included here.

Dr. Spath wishes to acknowledge the continued help of Mr. A. Reeley ; also, especially in connection with the bibliography and index, of Mr. R. Baker and Mr. D. Phillips, and, with the cutting of micro-sections, of Miss P. Hammond.

W. N. EDWARDS,

July, 1949. *Keeper of Geology.*

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Incertae sedis

Incertae sedis

INTRODUCTION

When Part IV was brought to a close, the few remaining groups of Ceratitida offered unexpected difficulties, especially an accumulation of genera which were claimed to be Hungaritidae. Their separation proved troublesome, not only because the classification here adopted is different from that given in the text-books, but also because it had to be brought into line with what had already been stated in the earlier chapters of this Catalogue, before the writer's views had crystallized in the scheme set out below. The proposed transfer of the genus *Reiflingites* (see p. 462, Part IV) from Ceratitidae s.s. to Danubitidae is one of the minor adjustments, and the temporary inclusion in Hungaritidae of a few still doubtful genera, as mentioned below, seems the most practicable solution of one of the remaining difficulties.

The other super-families of Triassic Ammonoidea are, by common consent, if under different names or groupings, the Trachyceratida, the Tropitida, the Arcestida, the Ptychitida and the Pinacoceratida. Their classification proved somewhat less complicated because there is less disagreement among authors than in the case of the Ceratitida. There are few modern attempts at classification, except the rather modest schemes of Pakuckas (1928) and Arabu (1938) ; and a number of Middle and Upper Triassic ammonites are still referred to groups here believed to have been long extinct, such as the Eotriassic families Dinaritidae and Tirolitidae. It was not always easy to suggest probable alternative relationships for these presumed homeomorphs of the older types. On the whole, however, the classification of the remaining super-families of Triassic Ammonoidea does not differ so very much from that used by the great masters of the past, notably Mojsisovics and Diener. One change consists of the re-introduction of the Lobitida Hyatt, dating from 1900, as a super-family instead of merely as a sub-group of the Arcestida (see p. 10 of Part IV). The number of super-families, therefore, is now eleven, and there is also an increase in the number of genera, as listed below. In Part IV the number of genera and sub-genera was 152 ; the present volume contains 236, making a total of 388, as compared with 247 in 1915, and 270 in 1933, according to Kutassy or 259 in Diener (1925).

It is hoped that the evidence from thin sections of the nuclei of a number of Triassic ammonites, incorporated in the systematic text below, will prove of general interest. Owing to technical difficulties and lack of suitable duplicate material in many genera, the use made of this line of research has so far been restricted, but it may be said at once that the exaggerated hopes placed on these investigations by some observers have not been realized. Our knowledge of the relations between the Carboniferous goniatites and the main stocks of Triassic ammonites is still largely conjecture. Miller and Unklesbay (1943) provided a useful addition to our knowledge by publishing micro-sections of a number of Permian ammonoids and it is interesting to note that they also conclude that "the siphuncular structures do not have as much taxonomic value as do the sutures." They record only two Permian genera in which the siphuncle is not external, namely *Agathiceras* and *Neoaganides*. The former has already been referred to in Part IV (p. 17), and since it has been suggested that I undervalued the importance of the siphonal features and considered them too variable to be used for systematic subdivision of the Ammonoidea, I may add that this genus *Agathiceras* is indeed a paragon of constancy (see p. 120). Yet Böhmers (1936) assigned seven species of the Carboniferous-Permian *Agathiceras* to seven distinct genera, although in four of them the internal structure was admittedly unknown. The great Mojsisovics, in the final decades of the last century, never subdivided to that extent. I am not objecting to subdivision as such, if it be based on, say, the development of the suture-line. This enabled us to derive *Agathiceras* from a *Proshumardites*-like ancestor and eliminated those imaginary *Paralegoceras*- and *Schistoceras*-stages of J. P. Smith. But I am not disposed to accept super-families based entirely on the position of the siphuncle in median sections, if this position can move as irrationally as in that Hungaritid described on p. 24.

The great majority of Lower Triassic ammonites have an external siphuncle, a notable exception being *Owenites* (Part IV, p. 184) in which it has been found by Böhmers (1936) to be centro-ventran in a Timor species (*O. egrediens* Welter). A section of the genotype, *O. koeneni* Hyatt & Smith, from

California (at 21 mm. diameter) prepared by the writer, confirms the centro-ventran position of the siphuncle. The siphuncle is central at the start, according to Böhmers, and remains well away from the ventral side of all the whorls in both species. In *O. koeneni* the thickness is as much as 30 per cent. in the third whorl and 20 per cent. in the fourth ; and the distance from the venter (30 per cent. of the whorl height in the second case) seems even less in the third whorl (20–25 per cent.), but the section is not quite central and the coarsely crystalline matrix of the Californian form is less favourable and more opaque than that of the Lower Triassic ammonites from Timor I sectioned previously.

But it is in the Middle and especially the Upper Triassic that the vagaries of the siphuncle become apparent, though, perhaps, not so common as in the Jurassic and Cretaceous. When I first directed attention to the instability of the siphuncle in young Carboniferous goniatites, I was categorically told that such goniatites did not exist. After some years, of course, the fact that they do exist had to be admitted, not without characteristic reservations such as that my figure of a section of *Gastrioceras listeri* was "useless," though it showed the siphuncle as clearly as the sections published by Schindewolf. Since the present volume contains no illustrations, my readers will have to accept on trust, for the present, the observations I am offering on the sections of Triassic ammonites examined. I know as well as any other worker who has prepared such sections that the great majority are imperfect, and I see no point in stressing irregularities due to oblique or otherwise defective sections which are generally obvious to an observer. Since, however, we are as yet only at the beginning of this line of research and since not nearly enough ammonites, especially Jurassic and Cretaceous, have so far been examined in thin sections, I am not claiming that my views on the instability of the siphuncle be regarded as final.

Part IV of this Catalogue ended with the description of the *Ceratites* of the Germanic facies, and before it was printed Schrammen (1933) published another paper on these forms, with more new generic names and a few excellent illustrations. At the same time he announced that a large monograph on these *Ceratites* was completed but could not be published on account of adverse economic conditions. Opinions may differ on whether this splitting up of the old *Ceratites nodosus* and a few allies into over 140 species is justifiable on stratigraphical grounds. The limestones of the Upper, Middle and Lower Ceratite Beds have been grouped into seven zones, of which, for example, the lowest has not only seven known species of *Ceratites* as zonal indices, but another 18 unnamed new species. Quite apart, however, from the stratigraphical value it is probable that the mere illustration of such a mass of material, under whatever names, would have meant an advance in palaeontological knowledge. Schrammen, of course, did not admit transitions between species and, as already mentioned (Part IV, p. 466), his conception of the origin of the species of *Ceratites* is highly improbable. But it remains to be seen whether or not the three simple divisions of the typical *Ceratites*, given in Part IV, convey a truer picture of a bewildering mass of closely connected forms than Schrammen's excessive detail.

When Mojsisovics illustrated a large number of apparently similar forms of *Trachyceras* on a very lavish scale in his two monumental works on the Cephalopoda of the Mediterranean Triassic Province and on those of the Hallstatt Limestones, the richness of these ammonite faunas astonished the scientific world and it was not till after many years that critics began to complain that the differences between certain species seemed very slight, and that Mojsisovics's classification was arbitrary and often inconsistent.

The writer has perhaps had more opportunity of using Mojsisovics's two magnificent works than many who consult this Catalogue, and it will be found that whenever it was considered necessary to emend an admittedly polyphyletic genus, or adjust some other groupings, such alterations were proposed without a feeling of escape from a tyranny "under which we have suffered long enough" (Wepfer, 1913). A thorough revision of Mojsisovics's material would perhaps result in the suppression of some species, though that is a trifling matter; but few genera could be rejected altogether, and the remainder, remoulded or left unchanged, would be just as elastic as they are now, for as Wepfer himself says: "Everything in Ammonites is in a state of flux." A return to the trinomial nomenclature of Quenstedt, if it were legally possible, would certainly not solve our difficulties, or provide that certainty of finality in our classification that some critics consider so desirable, but which will never be attained.

Among the more recent acquisitions of Triassic cephalopods, a collection made by the Anglo-Norwegian-Swedish Expedition of 1939 to Spitsbergen deserves special mention. Owing to the war, the collection was not received until late in 1947, and the specimens are as yet only partly named. Those of the Middle Triassic are referred to below, e.g. the *Nathorstites* and their associates ; but there are many Lower Triassic *Arctoceras* still awaiting determination. Associated with them in the same hand specimens are fragments of a large new *Flemingites*, already announced in 1921 (and referred to in Part IV, p. 116), that are of special interest. The Spitsbergen form must have been of much larger dimensions than any of the Salt Range examples which, moreover, are much more compressed and more finely ornamented. The longitudinal lineation, which is the only ornamentation present on these fragments, is rather coarse. On the smaller examples there are about 15 of these lines and they are distinct enough on the inner whorl side to be called longitudinal ridges. On an almost smooth cast of a body chamber (of a whorl height of 110 mm. and a roughly similar thickness) only 6 or 7 of these lines are left. The first and most distinct is about 20 mm. from the umbilical suture, the next four at intervals of 10, 12, 12 and 10 mm., and the last two are so faint as to be scarcely measurable, but the widely arched periphery is completely smooth, without that very indistinct siphonal depression that appears to border the 15th ridge in the smaller specimens.

On account of the coarseness of the longitudinal ornament and the unusual inflation of the whorl section, the fragments could easily be mistaken for body-chambers of nautiloids, but one shows the last septal surface and after that one or two incompletely-formed suture-lines. The three entire saddles and ceratitic lobes are almost exactly like those of *F. compressus* figured by Waagen (1895, pl. xvi, fig. 1*c*), but the straight, prionidian umbilical portion is much longer, the whole line in that fragment being about 75 mm., measured from the centre of the median saddle in the external lobe to the umbilical suture. The cast of another very large air-chamber has a suture-line, 145 mm. long, in which the second lateral and the auxiliary lobes have only three unequal terminal prongs, and the prionidian umbilical " saddle " is much shorter than in the first fragment. Moreover, the spiral lines are faint and close already on the chambered portion, five being visible within 16 mm. from the umbilical suture. These are followed by traces of two ridges at 25 and 45 mm. ; then the sides seem entirely smooth for about 65 mm., and it is only on the periphery, i.e. from 110–145 mm. that traces of four or five more spiral lines occur. There is only superficial resemblance to the body-chamber fragment of *F. cirratus* (White), figured by Smith (1932, pl. 20, fig. 1), which has a compressed whorl-section.

The fragments of *Flemingites* are from the nodules of the Fish-bed in which *Arctoceras* is by far the most abundant element. The other ammonites include only two forms (apparently new) of that *Wasatchites-Gurleyites-Arctoprionites* assemblage figured in Part IV ; a fragment of a *Keyserlingites* (*subrobustus* group) ; three *Xenoceltites spitsbergensis* Spath ; four *X. gregoryi* Spath ; three *Prosphingites spathi* Frebold ; one *P.* sp. nov., one *Parapopanoceras* ? sp. ; one *Tellerites*. It is very probable that this assemblage is of post-Flemingitan age, i.e. Upper Eo-Triassic, as *Euflemingites* (Part IV, p. 115) was believed to be of later age than the true *Flemingites*.

Another collection of Anisian cephalopods was recently presented to the Museum by Dr. F. T. Ingham, the Director of the Geological Survey of Malaya. The specimens are from the Budu Estate, Pahang, and although their preservation is very defective, such common Anisian genera as *Paraceratites*, *Acrochordiceras*, *Ptychites*, *Sturia*, etc., can easily be recognized. The fauna is very similar to that described by Diener from the Himalayan Muschelkalk, especially in the numerical preponderance of the forms of *Paraceratites* and allies. There seems to be less close affinity with the Anisian fauna of Timor, described by Welter (1915). The numerous examples of *Atractites* and (or) Orthoceratids in the same rock are crushed and indeterminable.

PART II.—SYSTEMATIC

V. Super-family CERATITIDA (*continued*).

Palaeontologists who used Part IV of this Catalogue may have been wondering why it included only part of the great super-family of Ceratitida. There were well-known types like *Balatonites* and *Hungarites* already characterized (on p. 382) as offshoots of Ceratitidae ; while *Danubites* (= *Florianites*) was also stated (on p. 463) to be related to *Reiflingites*, already described. These three groups might thus well have been dealt with at the same time and a few doubtful genera like *Apleuroceras* Hyatt (originally forming the isolated group of *Ceratites nudi* in Mojsisovics) and *Epiceratites* Diener (comprising Upper Triassic dwarf-forms of uncertain affinity) could have been added *incertae sedis*.

A good deal of research, however, remained to be done and there was doubt about some of the Ceratitid genera that clashed with families not yet studied in detail. One difficulty was the systematic position of the genus *Danubites* (= " *Florianites* ") in relation to the Celtitidae ; and the affinities of the genus " *Proteites* " (*recte Proteusites*) were altogether doubtful until the family Ptychitidae was studied. Similarly the Hungaritidae proved far more complicated a family than was anticipated, as will be seen below. Apart from these few Ceratitids, however, the remaining super-families of Triassic ammonoidea could be dealt with more or less according to the original plan.

Before continuing the systematic descriptions I may add that another doubtful Ceratitid, namely *Stacheites webbianus* Diener (1907, pl. v, fig. 6), referred to in Part IV (p. 267) as an entirely new stock, is now believed to be a reduced form of *Semiornites*, already described (p. 455). Since the spiral ornamentation and simple suture-line, however, are rather distinct, and since *Semiornites* itself has not been found in the Himalayan Middle Triassic, the species may yet be separated generically on the discovery of additional material.

Then the genus *Epiceratites* Diener, 1915*a*, based on *Amm. elevatus* Dittmar (1866) was said to include dwarfed " Ceratitids " with sigmoidal costation and rounded or elevated, smooth venter, sometimes bordered by two rows of ventrolateral clavi. It is almost certain that the forms listed by Diener as *Epiceratites* do not belong to one homogeneous group; and two of them, in any case, have been transferred by Kutassy (1933) to the genus *Metatirolites.* The remainder are now discussed under the family Buchitidae (p. 76).

The rare genus *Bosnites* Hauer, 1896 (genotype: *B. clathratus* Hauer, 1896) should have been added to the family Noritidae (Part IV, p. 274). It is represented in the Collection by three examples of its two species. The resemblance between *Bosnites* and *Norites* did not escape Hauer, but was perhaps too obvious to be accepted as proving affinity. Mojsisovics grouped *Bosnites* tentatively with the family Gymnitidae; and even Diener, while criticizing this view, did not express a more definite opinion as to the real relationship of *Bosnites.* Hyatt had it in Arpaditidae, though with a query; Smith even in Carnitidae, perhaps on account of the adventitious lobes. This breaking up of the external lobe is characteristic of the Noritidae, and the general plan is more important than the details. The fact that the suture-line is inverse, instead of straight, is not considered of systematic significance. When the ends of the lobes begin to touch the tips of the saddles of the previous septum, as a result of overcrowding, they often have to adapt themselves to the available space.

The genus *Hesperites* Pompeckj (1895), created for the unique *H. clarae* of the same author, has no place in the writer's classification; but even separation into a distinct family would not solve the problem of its anomalous position among the Triassic ammonites. I am not impressed by the differences of its Schlotheimid suture-line, adduced by Pompeckj; they apply to the one form he figured and "*Hesperites*" may not even be an early *Schlotheimia.* But until more specimens are found, and found *in situ*, associated with undoubted Rhaetic ammonites, it seems best not to accept *Hesperites* as a Triassic genus.

Another genus already referred to as being too incompletely known to allow of satisfactory classification is *Pseudharpoceras* Waagen. The original ammonite on which this genus was based, i.e. *P. spiniger* Waagen, 1895 (p. 130, pl. xxi, fig. 1) is unique and badly worn. It may be an Upper Liassic Hildoceratid, for the simple suture-line is obviously weathered and quite unreliable. In any case, there is strongly falcoid ribbing, with distant umbilical tubercles, as in some forms of *Lillia* and allied genera. Since the Salt Range form, moreover, came from some doubtful bed at the top of the Triassic sequence, the genus *Pseudharpoceras* may safely be rejected.

Now Smith (1932) adopted this name for a Lower Triassic form, described as an aberrant member of the Hungaritidae and therefore kept back when Part IV was prepared. The Idaho species certainly cannot be included in any known genus and therefore requires a new name. I suggest the new genus **Pseudarniotites** gen. nov., type to be *Pseudharpoceras idahoense* J. P. Smith, 1932 (p. 81, pl. xlix, figs. 17–19). The figured example represents a small, quadrate-whorled serpenticone, with strong, almost straight ribbing and well-developed carinati-sulcate venter. The suture-line is very distinctive, whether the principal lobe be entire or faintly serrated. There are only few elements and deep external and internal lobes.

This suture-line alone would prevent inclusion of the American form with *Pseudharpoceras*, if such a lower Triassic stock really existed. Both are rather out of place in the family Hungaritidae. Morphologically, *P. idahoense* might be thought to fall within the genus *Judicarites*, but the suture-line again prevents closer comparison. The species was also described as being more robust than *Tropiceltites praematurus* Arthaber (1911, p. 268, pl. xxiv, figs. 9–10) a form "evidently belonging to *Pseudharpoceras*." That genus (*Tropiceltites*) is ruled out by its age alone, and the new genus cannot thus be definitely referred to any known family of Triassic ammonites.

H. Family CERATITIDAE Mojsisovics, emend. (*continued*).

The few genera discussed below are close to some of the Ceratitid groups already described in Part IV and they are now transferred to the present family from the Hungaritidae with which they had been previously classed. For the Ladinian genotype of *Hungarites* is untuberculate and although the ribs are not robust and may have tended to weaken and disappear altogether, that genotype species could not have given rise to a form like *H. yatesi* Hyatt & Smith, which was smooth already in the earliest Anisian. The separation of Hungaritidae from the Ceratitidae will thus always be more or less arbitrary.

The genus *Halilucites* Diener, 1905*b* (genotype : *Ceratites rusticus* Hauer, 1896) was created for the arietiform *Hungarites* which are such a characteristic element of the Bosnian Middle Triassic. That they had been recognized as transitional was evident from Hauer's description of the genotype species (p. 259, pl. ix, figs. 1–4) as well as its allies (pls. ix–xi) as *Ceratites* (*Hungarites* ?). There is a small assortment of about a dozen of these forms in the Collection, and the more tuberculate species are distinctly reminiscent of *Paraceratites* and *Kellnerites*.[1] They are thus well separated from the already strained family Hungaritidae.

There seems to be a perfect passage from the typical *Halilucites* (e.g. *H. rusticus* and *H. arietitiformis*) through forms like *H. obliquus* and *H. intermedius* to the more discoidal types like *Ceratites* (*Hungarites* ?) *boeckhi* Hauer *non* Roth,[2] and thence to the almost normal *Hungarites plicatus*, all of Anisian age. It may thus well be held that the Ladinian genotype of *Hungarites*, i.e. *H. mojsisovicsi* Roth, is an end-form of this lineage. Since the genus, of course, includes many other species, it must be polyphyletic ; that is to say, it is admitted to represent an assemblage of Ceratitid offshoots tending to close the umbilicus and develop smooth, discoidal oxycones, like many Ammonitic stocks of the Lower Lias.

Another genus that should be included here is *Eudiscoceras* Hyatt, 1877 (for *E. gabbi* Meek, 1877, p. 128, pl. xi, fig. 4) representing a less coarsely ribbed edition of the *Halilucites* type. Smith (1914) who merely reproduced the original figure and presumably could not match the unique holotype among his prolific Nevada material, included it in *Paraceratites* and thought *P. gabbi* probably belonged to the group of *P. elegans* (Mojsisovics). This, however, is doubtful ; and in the decline of, first, the lateral tubercles, and then, of the ribbing as well, *Eudiscoceras* forms a distinct group of Ceratitids, transitional

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[1] The name *Popinites* Salopek, 1915, was used in Part IV (p. 458) instead of *Kellnerites* Arthaber, 1912*a*, also cited. It was, of course, assumed that the former name was substituted in place of the latter because it was preoccupied and I was at first surprised at Arthaber's complaint (1935, p. 94). But in 1936 (p. 176) Salopek himself used *Kellnerites*. *Popinites*, of course, must be rejected as a synonym.

[2] *Ceratites boeckhi* Roth was established in Böckh (1874, p. 175, pl. iv, fig. 13). Hauer's *C. boeckhi* therefore was stillborn and according to the Rules cannot be brought to life, even if we now include it in the genus *Halilucites*. The new name, *H.* **discus** nom. nov., is therefore now proposed for it.

to Hungaritidae. The keel in side-view, is obscured by compression, in the rock, between the two outer rows of clavi, but it is not as prominent as that of *Halilucites*.

The genus *Eutomoceras* Hyatt, 1877 (for *E. laubei* Meek, 1877, p. 126, pl. x, figs. 8, 8*a*) includes discoidal, rather involute, strongly keeled platycones, with ribbed and robust *Gymnotoceras*-like early volutions, but flattened outer whorls tending to degeneration of the (typically multipapillate) costation and final smoothness. The suture-line is ceratitic.

Hungarites and *Eutomoceras* had generally been kept apart, and whilst Hyatt (1900, pp. 554–7) put them into entirely distinct sub-orders, Diener, in his latest classification (1925, pp. 84, 86), also referred the former genus to the family Meekoceratidae, but *Eutomoceras* to the Ceratitidae.[1]

I cannot agree with J. P. Smith in considering *Eutomoceras* and *Halilucites* to be so closely allied as to include the latter, as a subgenus, in *Eutomoceras*. It is probable that the typical *E. laubei* represents merely a more specialized development of the same *Paraceratites* stock that also produced *Halilucites*, but the inner whorls of the typical species of the two stocks are sufficiently distinct for generic separation. The resemblance of *Eutomoceras* (*Halilucites*) *dalli* Smith (1914, p. 64, pl. xxix, figs. 1–4) to the Bosnian forms is considerable ; yet the true *Halilucites* are never papillate and are probably a local though not common Alpine-Bosnian element. The American *Eutomoceras* (which are fairly well represented in the Collection) are sufficiently distinct for generic separation. "*Hungarites*" *fittingensis* Smith (1914) was compared to the Bosnian *H. plicatus* Hauer, but it lacks its ventro-lateral shoulders and the large body-chamber example figured by Smith in pl. xc, and described as the type, appears to be a large *Eutomoceras*, with decline of multipapillate ornamentation. This is another instance of the difficulty of separating "*Hungarites*" from the other Ceratitida.

Eutomoceras, in fact, is another group that produced its own Hungaritids, like *Halilucites*. The genotype is distinct enough, with its small umbilicus and loss of ornamentation ; but one of the examples figured by Smith (pl. xxvi, figs. 7–8) with open umbilicus might have been attached to *E. breweri*,

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[1] For a reviser of the whole scheme of classification of the Ammonoidea of the Triassic Arabu (1938) seemed unduly mystified by the long-standing confusion between *Eutomoceras* and the entirely unrelated genus *Discotropites* Hyatt & Smith.

a species that was considered to be very closely allied to the Mediterranean *Halilucites discus*, above mentioned. *E. lahontanum* Smith, however, with its prominent tubercles is without any resemblance to Hungaritidae, so that *Eutomoceras* is now included in the Ceratitidae.

Another typical Hungaritid offshoot, is represented by an unnamed Spitsbergen group of ammonites referred by Frebold (1929) to *Eutomoceras*, but less ceratitid, including discoidal oxycones that recall the Jurassic genus *Leioceras* Hyatt (*opalinum* group). The three examples figured by Frebold (pl. ii, figs. 5–7) are poorly preserved and seem to differ among themselves as much as they differ from *E. laubei* Meek ; but they are important from a stratigraphical point of view.[1] The group ranges from extremely finely ribbed types, indistinguishable in crushed specimens from *Amm. opalinus* Reinecke, to the form represented in Frebold's fig. 5 (a homoeomorph of a more strongly ribbed *Leioceras comptum*) and to the large form with smooth outer whorl (Frebold's fig. 7). In this both the early *Eutomoceras* or *Gymnotoceras* stage and the succeeding *Leioceras* stage are lost comparatively soon, but, as in the apparently identical *Amm. triplicatus* ? Sowerby of Öberg (1877, pl. ii, fig. 10),[2] the umbilicus appears misleadingly large owing to the crushing.

As this group requires a new name, I am proposing for it **Koptoceras,** gen. nov.[3] (genotype : *K.* **falconi**, nom. nov. = *Eutomoceras* aff. *laubei* Meek ; Frebold, 1929, pl. ii, fig. 7) with *K.* **undulatum,** nom. nov. (*ibid.*, fig. 5) as a companion species. In the second form (B.M. No. C. 40583) the stage with sigmoidal, opaliniform ribbing ends at about 30 mm. diameter ; in *K. falconi*, entirely smooth on the outer whorl at 60–70 mm. diameter, the early, ribbed stage is confined to the innermost whorls (B.M., No. C. 40582). The suture-line, unfortunately, is unknown, but almost certainly ceratitic, as in *Eutomoceras*.

It may be held that this group is too incompletely known to be raised to generic rank ; but it is at least equally objectionable to use misleading provisional names for forms of strati-

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[1] The group first appears about 25 ft. up in the Middle Triassic "Oil Shale Series," but at 50 ft. from the base is absolutely dominant (at Keilhau Bay, east of Whales Point, Edge Island). The only other ammonite found was a crushed *Ptychites* cf. *oppeli* Mojsisovics.

[2] The second example, mutilated and badly drawn (fig. 11) is probably indeterminable.

[3] Not taken to be invalidated by *Coptocera* Murray (1868).

graphical importance. There is a motley assortment of such forms from Spitsbergen, coming from what must be a great thickness of Anisian and Ladinian beds, but so far known mostly from loose blocks or stray collections.[1] It is only their usual defective preservation as crushed impressions that has prevented their recognition as new and distinctive, if perhaps local, elements.

I. Family DANUBITIDAE nov.

When I stated (Part IV, p. 132) that *Preflorianites* was probably close to the stock from which sprang the Anisian *Tropigastrites* as well as the family Celtitidae, I still accepted the latter, more or less in Hyatt's (1900, p. 558) meaning, that is to say, this family was believed to represent a more or less homogeneous assemblage, ranging from the Anisian to the Norian, though some of the later members of that series were clearly more allied to Tropitids. *Danubites* Mojsisovics (1893), however, is now definitely separated from the Celtitids (see p. 96), and Hyatt & Smith (1905, p. 164) correctly stated that *Celtites floriani* Mojsisovics (1882), Hyatt's type of "*Florianites,*" had already been used as type of *Danubites* by Mojsisovics (1893); yet the latter author himself, at a later date (1902*a*, p. 323), adopted Hyatt's name "*Florianites*" and wrongly restricted *Danubites* once more, this time to the doubtful group of the Arctic "*Ceratites obsoleti*" (see Part IV, *Xenoceltites*, p. 128). This changed view was echoed by Diener in 1907 (p. 42); but in his Catalogue (1915*a*, p. 115) the same author correctly listed "*Celtites*" *floriani* as the genotype of *Danubites.* Such a form as *D. kansa* Diener (1895*b*, p. 103, pl. xxix, fig. 1), for example (represented in the Collection by a very fine Kashmir example, No. C. 28636), and the typical tuberculate *Reiflingites* are really rather distinct. This is suggested in spite of what has been said (on p. 463, Part IV) concerning the difficulty of identifying fragmentary material and in spite of Kraus's (1916) identification of *Reiflingites* with

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[1] The *Koptoceras* fauna at 50 ft. is followed, at 100 ft., by a *Gymnotoceras laqueatum* fauna (see *Ceratites* sp. indet. Frebold, 1929, pl. iii, fig. 9) with a large *Beyrichites* of the type of *B. verae* Frech (1903) and the Ceratitid figured by Frebold (pl. ii, fig. 2) as *Ceratites* (? *Hollandites*) sp. indet. This is too involute a genus for the Spitsbergen form, but the flattened periphery is much like that of *Hollandites arjuna* Diener (1895*b*). At 130–150 ft. come the first flattened *Nathorstites* or *Parapopanoceras*, with more small *Gymnotoceras* (?) and then, from 150–270 ft. the full development of good *Nathorstites*, as mentioned on p. 145.

Danubites (= "*Florianites*"). In view of the resemblance already noted (pp. 393 and 401) of *Danubites* to certain Acrochordiceratids it is even considered preferable to refer the former to a separate family within the Ceratitida, like the Hungaritidae and Balatonitidae. But *Reiflingites* which is at least as close to *Danubites* as it is to *Bulogites* will have to be transferred to the present family. It is not, however, here considered to be merely a sub-genus of *Danubites* (or *Celtites* in Frech, 1907*a*), but accepted as an independent genus. *Japonites*, which has also been described as a sub-genus of *Danubites*, is discussed below (p. 171) under Gymnitidae.

The Himalayan *D. kansa* Diener, already mentioned, and some fine Timor examples of the group of *D. alternecostatus* Welter (1914) are typical and these have a smooth, uncarinate periphery to a diameter of 110 mm. But there are 19 specimens in the Collection from Bosnia and Montenegro and they include such typical species as *D. retrorsus* (Hauer), *D. floriani* and *D. josephi* (Mojsisovics) and *D. intermedius* (Hauer) as well as apparent transitions to *Reiflingites*. The large examples of the type of *D. fortis* and *D. michaelis* (Mojsisovics) at over 90 mm. diameter lose the keel and the square venter, and develop a concave periphery. They then look quite different from the typical *Danubites*, but there is not one true *Reiflingites* with branching or tuberculate ribs.

The genus *Pseudodanubites* Hyatt (1900) was created for the Indian *Danubites dritarashtra* Diener (1895*b*) which differs from the typical forms in having a slight keel and in having a somewhat more advanced suture-line, with a more elaborately subdivided, not just serrated, first lateral lobe. The whorls are low and polygyral, and the slow coiling as well as the general resemblance to the genus *Tropigastrites* suggested reference to the family Celtitidae (Part IV, p. 127), but the short body-chamber and the long air-chambers support the affinity of *Pseudodanubites* with the true *Danubites*. Why Hyatt included it in the family Ptychitidae is difficult to see, though association with *Japonites* may have been prompted by the reference to that genus of forms like *Sibyllites planorbis* Hauer (*Tropigymnites*, p. 102), another keeled Celtitid, like *Tropigastrites*.

J. Family BALATONITIDAE nov.

This assemblage, now raised to family rank, covers widely umbilicate, more or less serpenticone Ceratitids with strong ornamentation, smooth, rounded, fastigate, or keeled venter, constrictions or more rarely tubercles, and simple ceratitic suture-line, sometimes reduced to only one large lateral lobe. There is no connection with the Trachyceratidae, as Mojsisovics and Haug thought at one time.

This family comprises only the three genera, *Balatonites*, *Judicarites* Mojsisovics, and *Cuccoceras* Diener. The first dating from 1879 (genotype: *Trachyceras balatonicum* Mojsisovics, 1873, p. 426, pl. xiii, figs. 3–4) comprises highly ornamented forms with extremely variable tuberculation, generally arranged in umbilical, median and ventro-lateral rows, with sometimes a siphonal row, forming a crest on the more or less fastigate periphery. Suture-line simple, ceratitic, with only two lateral lobes, often interlocking.

The varying degree of development of the three or more rows of tubercles, and the changes in the periphery, from mere rounding or chevrons directed forwards to a high crest, have resulted in this genus having more than its proper share of species, but they are mostly mere varieties of a few typical forms and even these are very closely allied. Thus the many species of *Balatonites*, recognized by Arthaber (1896*b*) in the Reifling Limestone of Styria, can be reduced to a few fundamental types, and the fine series of 37 Bosnian *Balatonites* in the Collection, show that most, if not all, of these species are connected by transitions.

The Salt Range "*B.*" *punjabiensis* Waagen (1895, p. 64, pl. xxiv, figs. 5*a–c*) is still as doubtful as when Philippi (1901, p. 104) thought it to belong to an unknown genus. Knowing the preservation of the ammonites of the Upper Ceratite Limestone, I am not prepared to express any opinion on this possibly quite imaginary figure.

The reference, to *Balatonites*, in Newton (1925) of a crushed Malayan example of, perhaps, "*Polycyclus*" *nasturtium* Mojsisovics, is difficult to explain. It was accompanied by the specimen of *Juvavites* (?) mentioned on p. 106. Another impression of an ammonite from Singapore was also labelled by Newton (1925) as "remotely resembling *Balatonites*," but it is quite indeterminable. It consists merely of a fragment of the umbilical border of a larger and more evolute ammonite, with traces of a few tubercles.

The genus *Judicarites* Mojsisovics (1896*a*, p. 697) was proposed for the "group of *Balatonites arietiformes*," so that the species *B. arietiformis* Mojsisovics (1882, p. 85, pl. xxxviii, figs. 1–2) becomes *ipso facto* the genotype. Diener (1915*a*, p. 165) cited *Ceratites euryomphalus* Benecke (1866) as the genotype of *Judicarites*, but that species merely happened to be the first to be described by Mojsisovics. The name replaces *Arniotites*, which was at one time believed to cover the group of *Balatonites arietiformes*; but Crickmay (1928) has shown that the genus *Arniotites* Hyatt, in Whiteaves (1889), is of Lower Liassic age. The Collection includes five examples of *Judicarites arietiformis* from Bosnia and two specimens of *J. euryomphalus* from the Schreyer Alm.

The Nevada *Balatonites hadleyi* Smith (1914, p. 119, pl. xc, figs. 8–10) was stated to be possibly a *Judicarites*, but it is quite unlike either genus, with its high, continuous keel and strong, lateral tubercles. It really requires a new name, but none of the American species of *Balatonites* is represented in the Museum.

The genus *Cuccoceras* Diener, 1905*b* (genotype: *Trachyceras cuccense* Mojsisovics, 1873*a*, p. 428, pl. xiii, fig. 1) was established for costate Balatonitinae with numerous constrictions and ribbing continuous across the narrowly rounded periphery. The suture-line has only the wide first lateral lobe conspicuously developed.

The presence of tubercles on the ribs in the Himalayan *C. yoga* Diener (1907, p. 85, pl. iii, fig. 7, pl. ix, fig. 4) shows that *Cuccoceras* and *Balatonites* are closely allied. Arthaber (1912*b*, pp. 341, 345), in his discussion of the systematic position of *Cuccoceras*, showed that it was intermediate between *Ceratites* and *Balatonites*, that all three genera occurred together in the Upper Anisian and that adult individuals had suture-lines of approximately the same degree of development. Apart from the presence of constrictions, the character of the periphery is the most obvious diagnostic feature.

K. Family HUNGARITIDAE Waagen (1895), emend.

Among the typical genera of this family there is, first of all, *Hungarites* Mojsisovics (1879*a*) itself, which has for genotype *Ceratites mojsisovicsi* Roth, 1871, p. 213 (= *C. zalaensis* Boeckh, 1873, pp. 150, 155, pl. vii, figs. 1*a*, *b* (lectotype)). It includes platycones, with high, median keel on a sub-tabulate periphery and ventro-lateral shoulders usually well-marked. There is sigmoidal ribbing, generally indistinct and often lost on outer whorls. The suture-line is ceratitic to sub-ammonitic.

Some forms included in this widely distributed genus, like the Californian *H. yatesi* Hyatt & Smith (1905, p. 129, pl., xx, figs. 1–4), are from the lowest Anisian ("*Parapopanoceras*" beds). There are as yet no real transitions known to the Eotriassic genera. The Ladinian genotype must, then, be taken to represent a later development of Ceratitids, perhaps of the Bosnian *Halilucites* of Upper Anisian age, although the latter tend to have a more sub-divided suture-line.

Among the Hungaritids in the Collection from the Gulf of Ismid (Asia Minor) are *Hungarites solimani* Toula (1896*d*, p. 176, pl. xxi, figs. 3*a*, *b*, 4 (lectotype)) and *H. propontícus* Toula (1896*d*, p. 176, pl. xxi, figs. 5*a*–*c* (lectotype) and 6*a*, *b*). These two species are connected by so many transitions that Arthaber (1914) thought it probable that they represented merely different stages of growth and individual variations of one form. Most of the specimens in the Collection, labelled *Hungarites solimani*, appear to me, in fact, to belong to *H. proponticus*. If the two species are now kept separate, it is done chiefly because the types figured by Toula show very obvious differences in the suture-lines.

The genus *Iberites* Hyatt (1900) was created for the Ladinian *Hungarites pradoi* (d'Archiac MS.) Mojsisovics (1882, p. 225, pl. xxxii, figs. 7*a*, *b* (lectotype), 8 ; pl. xxxiii, figs. 1–2) and includes platycones with fastigate periphery and ventro-lateral shoulders. The different examples figured by Mojsisovics show some variation and it is difficult to know exactly which character prompted Hyatt to separate *Iberites* from *Hungarites*. Mojsisovics stated especially that examples of the two genera of medium age were very similar. The genotype of *Hungarites* is non-tuberculate, but in the adult the body-chamber tends to lose the keel and ventro-lateral shoulders, and becomes rounded. In *Iberites* large examples may acquire lateral and outer tubercles and the keel remains very prominent to the aperture near which tuberculation may again be lost. The differences in the suture-line are also slight ; there are two lateral lobes in *Hungarites*, but three in *Iberites*, scarcely a difference of generic importance.

If *Hungarites yatesi* is as near to *H. pradoi* as Hyatt & Smith (1905) thought, then the range of *Iberites* is from the base of the Anisian ("*Parapopanoceras*" beds) to the Ladinian.[1] But

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[1] *Hungarites* cf. *yatesi* is said to have been found in the Ladinian of Mora de Ebro, Spain, together with *Iberites pradoi* (*fide* Wurm (1913) and M. Schmidt (1935)).

Iberites is not the equivalent of what some authors (e.g. Frech, 1903; Bubnoff, 1921) called the leiostracous Hungaritids. The genotype itself belongs to that group, and *Iberites* is at most a morphological genus, but not a true lineage. *Hungarites* is altogether a most variable assemblage, with trachyostracous forms occurring throughout the higher Anisian and Ladinian side-by-side with the smooth types. Hence we get passage-forms to the typically more carinatisulcate *Halilucites* on the one hand, and, by way of *H. rothpletzi* Salomon, and *H. waageni* Mojsisovics, transitions to *Balatonites* on the other.

The lower Anisian genus, *Noetlingites* Hyatt, 1900 (for *Ceratites strombecki* Griepenkerl, 1860, p. 161, pl. vii, figs. 1–3), is represented in the Collection only by a plaster-cast of the holotype from the Lower Wellenkalk of Silesia. It has a fastigate periphery throughout, unlike *H. mojsisovicsi*, the genotype of *Hungarites* which has a pronounced keel before the terminal rounded stage, but, like *Iberites*, *Noetlingites* is closely connected with the typical forms of *Hungarites*. The ceratitic suture-line of *Noetlingites* has only three lobes, broadly rounded saddles, and no median saddle in the external lobe.

The genus *Carnites* Mojsisovics, included by Hyatt in the family Hungaritidae, is here referred to a distinct family. Hyatt, it may be remembered, had the Hungaritidae in the super-family Pinacoceratidae, together with Ptychitidae and Gymnitidae, but that classification is not here adopted. The Himalayan *Hungarites* in the Collection, figured by Salter (1865), are referred to below under Carnitidae.

INCERTAE SEDIS.

As here restricted, the family Hungaritidae comprises Anisian-Ladinian offshoots of the Ceratitidae. The three genera discussed below are therefore included here only because they have all been referred to this family, either by their authors or by more recent revisers. As will be shown, *Arctohungarites* may be referable to the family Arctoceratidae rather than to Hungaritidae, while *Dalmatites* may be a keeled offshoot of a Dinaritid stock. *Prohungarites* is quite uncertain, but could be connected with *Hanielites* (Part IV, p. 243), as mentioned below.

Oxycones are always end-forms, and they originate from root-stocks with rounded venters, often through carinatisulcate intermediaries. They may return to a secondarily arched condition on their body-chambers, as in *Arctohungarites* and *Dalmatites*. Thus the various waves of "*Oxynoticeras*" in the Lower and Middle Lias have never given rise to new stocks, but either reduced their suture-lines and modified their body-chambers (*Cheltonia*), or ran to extremes in size (*Gleviceras*, *Metoxynoticeras*) and finally disappeared (*Carixiceras*) before the Domerian Amaltheids produced oxycones of their own (*Amauroceras*). This production of oxycone end-forms went on to the end of the Cretaceous, but few palaeontologists would now group them together, as the early authors (e.g. Neumayr) did.

There is, first of all, the Lower Triassic, Siberian genus *Arctohungarites* Diener, 1916*e* (genotype : *Hungarites triformis* Mojsisovics, 1886, p. 87, pl. xi, figs. 15*a*, *b* (lectotype), 14*a*, *b*, 16*a*–*c*) and it includes platycones with obscure sigmoidal folds on body-chamber and distinct keel only on later chambered portion tending to disappear again towards the aperture in some forms. The suture-line is ceratitic, with deep external lobe and three prongs on each side of the low median saddle. The first lateral lobe is slightly longer, and there are a second lateral and two auxiliary lobes, all subdivided.

This small group is perhaps related to *Arctoceras affine* Mojsisovics sp. (1886, p. 86, pl. xi, figs. 17*a*, *b*), which again is connected with the contemporary *Submeekoceras* and *Meekoceras*. As in the case of several other keeled offshoots already discussed in Part IV, the mere acquisition of a carina in a normally unkeeled stock is not considered of great significance. Thus it is quite certain that the oxynote Permian *Discotoceras*, still included by Diener in *Hungarites* (1913, p. 24), has no connection with the Upper Eotriassic stock here discussed, and, as mentioned below under *Dalmatites*, these "Hungaritidae" are merely more or less homoeomorphous offshoots of yet unknown stocks.

A second Eotriassic genus provisionally retained in the family Hungaritidae (Part IV, p. 327) is *Prohungarites* Spath (1934), which was established for *Prohungarites similis* Spath (= *Hungarites* cf. *middlemissi non* Diener ; Welter, 1922*a*, p. 146, pl. clxvii, figs. 6–9, 18). It may be defined as comprising more or less involute, discoidal shells with irregular *Hungarites*-ribbing, continuous across the tricarinate or sometimes only faintly keeled periphery, but breaking up into striae on the venter. Suture-line ceratitic, with only two lobes. Body-chamber three-quarters of a whorl ; aperture with sigmoidal sides and slight rostrum.

One example of *P. similis* (No. C. 34193) was sectioned, but on account of the preservation, in crystalline calcite (with hollow air-chambers), it proved of little help. At 23 mm. diameter there were four whorls with septa (numbering 16, 14, 12 and 10, respectively, counting inwards) and a fifth innermost whorl with another 10 almost unrecognizable septa. The siphuncle was apparently external throughout, but only two funnels, pointing forwards, could be seen on the outer whorl.

It is doubtful whether the Kashmir "*Hungarites*" *middlemissi* Diener (1913, p. 23, pl. iii, figs. 5–7) is congeneric with the Timor species (well represented in the Museum) for which *Prohungarites* was created, as already mentioned on p. 244 (Part IV). But the Kashmir form is incompletely known. It differs from the genotype of *Prohungarites* in having its greatest whorl thickness (at a corresponding diameter) in the vicinity of the latero-peripheral edges. Its numerous smooth inner whorls may also suggest affinity with an Eotriassic stock, for the (caenogenetically) tuberculate *Hanielites* seems to be connected with *Prohungarites crasseplicatus*, by way of *Hanielites tuberculatus* (Welter), previously included (with doubt) in Kashmiritidae. The vertical umbilical edge of the species of *Prohungarites* (see p. 244, Part IV) is characteristic.

A third Eotriassic genus, retained in Hungaritidae only with doubt, is *Dalmatites* Kittl (1903*a*) created for *D. morlaccus* Kittl (1903, p. 73, pl. iv, figs. 4, lectotype, 5, 6, 7). It includes discoidal, involute, nearly smooth oxycones with simple ceratitic suture-line, showing three feebly toothed lobes and entire saddles.

This genus was referred by its author to Hungaritidae (Pinacoceratidae), by J. P. Smith (in Zittel, 1913) to Ceratitidae, by Arthaber, Haug & J. P. Smith (1932) again to Hungaritidae. *Dalmatites*, although retained in this family, is probably merely a keeled development of the same Dinaritid stock that produced *Stacheites* and *Pseudokymatites*. *Dalmatites* differs from *Stacheites* chiefly in its smaller umbilicus and in the presence of another lobe. On two of Kittl's examples (figs. 5 and 6) the outer whorls revert to a rounded periphery, but, although the ontogeny of *Dalmatites* is unknown, the keel does not seem to have been ephemeral, as, for example, in some Arcestids.

"*Dalmatites*" *ropini* Diener (1907, p. 93, pl. ix, figs. 5, 6), in spite of its simple suture-line, is probably closer to some

Anisian stock than to the true Eotrassic *Dalmatites*. It is probably separable, generically, and it could be a fore-runner of *Neodalmatites*.

Sub-family LONGOBARDITINAE nov.

The separation of this sub-family from the Hungaritidae is prompted by the desire to make that family a less heterogeneous assemblage, but it is doubtful whether the writer's view will receive assent from all palaeontologists. For, while *Longobardites*, in spite of its adventitious lobes, could be classed with the Anisian-Ladinian genera of Hungaritidae above listed, its equally multisellate ally or derivative "*Dalmatites*" J. P. Smith, *non* Kittl is rather distinct. *Longobardites* attaches itself quite naturally to the early *Hungarites*, with increase of the number of elements in the suture-line, like *H. yatesi* Hyatt & Smith (1905) from the lowest beds of the Middle Trias. The suture-line of *Longobardites* shows still greater complexity because it developed adventitious lobes, comparable to those of the somewhat homoeomorphous Eotriassic *Parahedenstroemia*.

As the suture-line of a young *Longobardites* shows (see J. P. Smith, 1914, pl. vi, fig. 18), the differences from the multisellate suture-line of "*Dalmatites*" *minutus* Smith (1914, pl. xxix, fig. 19) are slight and there are variations in the general curvature even within the genera. It was believed at one time that *Longobardites* and *Nathorstites* were connected by these Anisian forms, wrongly assigned to *Dalmatites*, and a failure to recognize their correct position was responsible for at least some of the difficulties experienced with the family Hungaritidae when Part IV was brought to a close.

The genus *Longobardites* Mojsisovics, 1882 (genotype: *Longobardites breguzzanus* Mojsisovics, 1882, p. 185, pl. lii, figs. 1*a*, *b*, 2), was created for involute oxycones, with faint sigmoidal striation. The suture-line is ceratitic, but shows a tendency to increase the number of elements. Mojsisovics thus grouped the genus with Pinacoceratidae, but the writer agrees with Hyatt & Smith (1905, p. 132) in considering the affinities of *Longobardites* to be with *Hungarites*, from which it differed in the possession of adventitious lobes and in lacking prominent "shoulder angles or keels." Later (1914, p. 50) Smith transferred *Longobardites* to the family Pinacoceratidae, but, as mentioned below, the curious resemblance to *Sageceras* may have misled him.

There is a possibility that the long-lived *Longobardites* may include at least some members of the family Beneckeidae in which Waagen included it already in 1895. That is to say, the Anisian forms of *Beneckeia* may be reduced Hungaritids (with secondarily entire suture-lines) and thus may not be connected with the Eotriassic species of that genus, with which they were associated (in Part IV, p. 234) in the family Hedenstroemidae.

The preservation of the specimens of *L. nevadanus* in the Collection (in a black, crystalline, limestone) is not favourable to the preparation of the suture-lines, but from Hyatt & Smith's fig. 18 (pl. xxv) it appears that the suture-line of the young has the external and the two lateral lobes of about the same depth. Later the first lateral lobe becomes the deepest, but in *L. breguzzanus* and *L. zsigmondyi* (see Mojsisovics, 1882, pl. lii, figs. 2 and 4) the saddles between these three lobes have different proportions. Whether this is due to variations in development of the adventitious lobes will have to be established by ontogenetic research; but the resulting similarity to the lobes of *Sageceras* is considerable. Judging by its unusual size, it appeared in fact that the example figured by Smith (1914), in pl. xxx, fig. 16, was not a *Longobardites* at all; and in any case its suture-line did not seem to agree with that of the small example illustrated in Smith's pl. viii, figs. 16–18. But a similar *Sageceras*-like example in the Collection, named by Prof. Smith himself, shows the characteristic bases of the lobes.

The Collection also includes some specimens of *Longobardites* (?) *parvulus* Reis (1901, p. 92, pl. iv, figs. 28–29 lectotype, 30, 31; 1907, p. 117, pl. i, figs 5–8), but they are rather small and poorly preserved. The suture-line of this form, if really a *Longobardites*, must owe its simplicity to secondary reduction. In any case, if only one or two lobes retained, or had acquired, a serrated base, they were more likely to be the principal, lateral lobes than the auxiliary lobes, as Reis thought.

Longobardites, then, is not believed to be connected with the true *Dalmatites* which (in Part IV, p. 327) I stated to be an Eotriassic member of the Hungaritidae. This, however, did not apply to the Anisian species described by J. P. Smith (1914) as "*D.*" *parvus* and "*D.*" *minutus*. A small example of the former, not showing the suture-line but from Prof. Smith's own collection, differed from specimens of *Longobardites* *nevadanus* Hyatt & Smith, from the same collection, merely in a slightly greater whorl-thickness. When, however, in 1927, the Museum acquired from P. Train a large collection of Nevada ammonites, a considerable number of these so-called *Dalmatites* were found and believed, after some hesitation, to be young *Nathorstites*. It was partly because some were actually associated in the same hand specimens with *Gymnoceras*, *Eutomoceras* and other Middle Triassic ammonites that reference to *Nathorstites* was queried, in spite of the general resemblance. Fortunately the Museum also received a number of Spitsbergen (Edge Island) examples of *Nathorstites*, associated with a few Cladiscitids. Many of these fossils were in an excellent state of preservation, so that a more detailed study of the genus *Nathorstites* could be undertaken than was possible at the time of preparation of Part IV. The resemblance, it may be mentioned at once, turned out to be quite superficial.

Now, in 1914, J. P. Smith suggested that his " *Dalmatites* " might be a simplified development of the more complex *Longobardites* of the same beds. This contention is supported both by the similarity of the radial line, with its peculiar reclined curve, and by the suture-line which ascends towards the umbilicus in " *Dalmatites*," but still shows a suggestion of the adventitious elements of *Longobardites*.

The length of the body-chamber in *Dalmatites* was given by Smith (1914) as two-thirds of a whorl, which agrees with what is shown in one of the largest Nevada examples of " *D.*" *parvus* in the Collection (diameter = 42 mm.). Few of the Nevada specimens again show the suture-line except where exposed by etching. But in at least one example the aperture is almost intact and shows a broad, lateral lappet, corresponding to the reclined radial line (of the adult) and a slightly raised ventral rostrum. The lateral edges of this are more or less radial, whereas only a few millimetres away from the end, the strongly reclined striae of growth meet the sharp keel at an angle of about 45°. The aperture thus must have been much like that of *Nathorstites*.

" *Dalmatites* " has a comparatively wide principal lobe and few elements to the outer half of the suture-line at a diameter at which *Longobardites* already has interlocking septal edges. This is the principal difference ; smaller differences were discovered when specimens were dissected and thin sections were prepared, and these revealed at once that not only was there no affinity with *Nathorstites*, but that there was sufficient reason for separating these "*Dalmatites*" with an independent generic name. As such I propose **Neodalmatites** gen. nov., type to be *Dalmatites parvus* J. P. Smith (1914, p. 60, pl. xxx, figs. 1–2).

In thin sections, *Longobardites* shows a much quicker increase in whorl-height than *Neodalmatites* and a general resemblance to such Ceratitids as *Eutomoceras*. The siphuncle is external from the start, as seen in two of the sections, but in others it is external, where seen, at various diameters. There are only about 8 or 9 septa to the whorl below 2½ mm. diameter and the height is increasing rapidly, so that after another whorl, the diameter is already 7 mm. There are, then, about 12 septa, rather irregularly spaced, but getting very close (about 28 to the whorl) on the last volution of three of the five slides. This corresponds with the external interlocking of the septal edges at larger diameters.

In *Neodalmatites*, on the other hand, the coiling is slower, and though the septa are very irregularly spaced, they are fairly close in the young (30–32 on the first 3 whorls in at least two sections) but they are less close than in *Longobardites* on the later whorls (12 on the last septate whorl of a specimen of 9 mm. diameter, and no approximation of the final septa). The siphuncle is also external, but could not be seen on the innermost whorls, except in one slide (out of eight), and then only at the beginning of the second whorl and throughout the third whorl. This section, however, shows only 8 septa on the first whorl and nine on the second, with 18 on the outer whorl, but only the last two septa approximate. The thickness of the siphuncle on the third whorl is ·2 mm., or one-sixth of the whorl-height, but the protoconch has a long diameter of only ·3 mm., as in *Tropites*. In both *Neodalmatites* and *Longobardites* the siphonal funnels are directed forwards as well as backwards on the outer whorls, but short.

One section provided a startling surprise, for, as in *Owenites egrediens* Welter, the wide siphuncle remained centro-ventran to the end of the septate stage. At 5 mm. diameter, that is after 3¼ whorls, the siphuncle was about one-sixth of the whorl-height (or just over its own thickness) away from the venter, and after one more whorl, at a diameter of 12 mm. the siphuncle was still in the same relative position. That this was the actual end of the shell was confirmed by the presence of the body-chamber as well as the last nine septa which became suddenly very closely spaced. All the siphonal funnels were directed backwards in this example.

The more rapid increase in whorl-height suggests that this section with a central siphuncle might have belonged to a young *Longobardites* rather than a *Neodalmatites.* At small diameters the two genera are very similar except in suture-line (which has to be exposed by treatment with acid) and the slight difference in thickness ; and in identifying the specimen sectioned as *Neodalmatites,* I may have relied on the presence of the *Nathorstites*-like pleats, the most obvious distinction from the smooth young *Longobardites.* But whether the slide represents *Neodalmatites* or *Longobardites,* it shows that in the Triassic, as well as in the Jurassic and the Cretaceous ammonites, the vagaries of the siphuncle are independent of whorl-shape (Spath, 1933*a*, p. 432). For the genera just mentioned are oxynote, whereas *Didymites* and *Lobites* (with a centro-ventran siphuncle) have globose shells and *Traskites* has a ventral groove.

There is a general resemblance of *Neodalmatites* to *Arctohungarites* even in the suture-line, but the latter has a wider umbilicus and the lateral folds are of a different nature. They are not now grouped together on account of the difference in age and because *Neodalmatites* is still more closely connected with the contemporary *Longobardites.*

The genus *Perrinoceras* Johnston, 1941 (genotype : *P. novaditus* Johnston, 1941) was originally described as being possibly a *Parahedenstroemia* (Part IV, p. 221), though its ceratitic suture-line has no adventitious elements. It is decidedly simpler than the suture-line of *Longobardites,* with a similar number of elements but a different external lobe ; in my opinion it confirms the longevity of the stock, for it is of Carnian age. Its companion species, " *Metahedenstroemia* " *desertorum* Johnston, on account of its bicarinate periphery and adventitious elements, is here referred to the family Carnitidae (see *Neoclypites,* p. 30). Both are very important additions to our knowledge of the Upper Triassic smooth oxycones which at one time were all included in the Pinacoceratidae.

L. Family CARNITIDAE Arthaber (1911).

This family is adopted for a group of discoidal ammonites of the Carnian which are here taken to be related to the old-established and spectacular, though highly controversial, genus *Carnites*. This group is believed to be distinct from the leiostracous Pinacoceratidae, with which family it had been classed by some, and being of Carnian age the group is taken to have nothing to do with the Norian genus *Hauerites*, with which others had united it in a family Haueritidae.

As is well-known, there are many Triassic ammonites with adventitious lobes. They are mostly discoidal, more or less oxynote types, with a narrowly truncate or sharpened venter and a small or closed umbilicus. But they may be derived from widely different stocks. Some have already been dealt with in Part IV ; some belong to the family Pinacoceratidae, described below ; some of the Middle and Upper Triassic types attach themselves to the Ceratitidae and others to the Trachyceratida. The adventitious elements of the suture-line, it may be mentioned, originate in different ways, either from the breaking-up of the median saddle in the external lobe, or of the external saddle, or both.

Thus the typical genus *Carnites* Mojsisovics, 1878 (genotype : *Ammonites floridus* Wulfen, 1793), at first considered by Mojsisovics to be a *Pinacoceras*, has one or two adventitious saddles between the external saddle and the siphonal line, according to size ; and there are a number of auxiliaries (at least six) in a series that is slightly dependent towards the umbilicus, but still centroserial in Diener's meaning. I accept Diener's opinion that *Carnites* and the oxynote *Pinacoceras mojsvari* Frech, of Wengen (Upper Ladinian) age are not related, in view of the totally different ontogenetic development of the suture-line in the two genera. To me, the strong ornamentation of the body-chamber of *Carnites nodifer* Diener is also evidence against closer connection between the genus under discussion and the family Pinacoceratidae. But I am not prepared to go back for the root-form of the family Carnitidae to the Eotriassic genus *Tellerites*, already dealt with in Part IV (p. 224) and referred to the Hedenstroemidae. This family, it is true, also has adventitious lobes, but they develop in quite different directions. Hyatt (1900) also separated *Carnites* from the Pinacoceratidae, but he included it in the Hungaritidae ; acting on recapitulatory principles, he may have been prompted merely by the presence of a median, ventral keel in the young of *Carnites*.

The connection of the genus *Carnites* with the Hungaritidae, and therefore the super-family Ceratitida, is partly due to the confusion by Salter (in Salter & Blanford, 1865) of certain Himalayan ammonites with the original *Amm. floridus*, and to the miscarried attempt by Mojsisovics (1896*a*) to identify Salter's forms from plaster-casts. Salter's collection of Triassic fossils from Niti is in the Museum and it includes the originals of the two *Hungarites* figured by Mojsisovics, as well as a number of additional, mostly fragmentary, specimens of the original *Amm. floridus*. Now, all these two ammonites have in common with the form figured by Mojsisovics, on the same page (as fig. 1), is the tricarinate periphery. As Diener (1908*a*) pointed out, the type of the species *Hungarites nitiensis*, and therefore of the genus *Rimkinites* Mojsisovics (1902*a*), can only be the small ammonite represented in fig. 1, with ammonitic suture-line. Salter's *Amm. floridus*, as represented by the originals of Mojsisovics's figs. 2 and 3, is much nearer the true *Hungarites* or *Longobardites* (the former in ornamentation, the latter in suture-line) and has in fact been renamed *Rimkinites edmondii* by Diener. But it is doubtful whether Salter's form is identical with the Thanam Valley examples figured by Diener, especially if their suture-line agrees with that of *R. nitiensis*, i.e. if it is brachyphyllic.

The suture-line of *Rimkinites edmondii* resembles that of *Longobardites* in the constriction, at the waist, of the long and slender principal saddles, while their tips remain entire, as shown in Salter's fig. 1*e*, which, however, is diagrammatic and inaccurate in many details. Thus the first lateral lobe is deeper than the external lobe and relatively wider, certainly wider than the second lateral lobe, which is scarcely more than half its length and narrower, with the second lateral saddle definitely shorter than the first, both the external saddle and the second lateral saddle being over-topped by the first lateral saddle. The first auxiliary lobe, instead of being, as in Salter's drawing, almost as long as the lateral lobes, is still shorter and narrower than the second lateral lobe, but the second auxiliary lobe, though short, is unexpectedly wide and has only two sharp and equal prongs. The third auxiliary lobe near the umbilical edge is similar, with the median protuberance at its base almost as prominent as another saddle. In Salter's drawing the umbilical portions of successive suture-lines may have been confused, and there is no justification for Mojsisovics's remark that the specimen had suffered through weathering.

The larger example (Mojsisovics's fig. 3 or Salter's fig. 1*d*) did not show a suture-line until developed by the writer. It agrees with the smaller example, on the whole, but the external lobe does not show the many digitations of Salter's drawing. Instead, there is just one relatively large protuberance at its base, as in *Rimkinites nitiensis*, with only two minute notches at the foot of the external saddle and one higher up, at about its middle. The difference between the large and deep first lateral lobe and the small second lateral lobe, not to mention the still more reduced first auxiliary lobe, is very marked. The second auxiliary lobe is shallow and seems already entire, while the third apparently would be divided by the umbilical suture, as in Diener's form. The latter has a whorl-thickness of 31 per cent. and an umbilicus of 12·5 per cent. of the diameter ; in Salter's two examples the corresponding proportions are 28 per cent. and 14 per cent., so that they may be taken to be at least very close allies, morphologically, even if the suture-line of the Thanam Valley form should prove to be more ammonitic than that of the typical *R. edmondii*, i.e. Salter's *Amm. floridus*.

It is clear that this species is intermediate between *Hungarites* and *Longobardites* on the one hand, and *Rimkinites nitiensis* on the other, all four of Ladinian age. In spite of this, Diener did not think that *Rimkinites* was "closely related" to *Hungarites*, and he considered the tricarinate venter a feature of generic distinction, whereas I can see no real difference in this character, but consider the suture-line sufficient for generic separation. Again, according to Diener, *Rimkinites* was no more closely related to *Carnites* than to *Hungarites*. It was true, he held, that in its ontogeny, *Rimkinites* "recalled" *Carnites*, but in the later stages of growth the two genera followed very different lines of development. In *Rimkinites* the tricarinate periphery persisted ; in *Carnites* it was lost and adventitious elements appeared in the suture-line. The ontogeny of the two genera, however, suggested to Diener that they were derived from a common root. *Rimkinites*, all the same, remains a probable connecting link between *Carnites* and *Hungarites*. This, of course, would make both *Rimkinites* and *Carnites* descendants of the great super-family of Ceratitida.

This association seemed unacceptable on account of the ammonitic suture-line of *Rimkinites* and *Carnites*, although a similar but less complex suture-line is found in *Beyrichites* and other genera here included in the Ceratitida. On the other hand, I can see no good reason for attaching *Carnites* to the super-family Trachyceratida. A certain resemblance to *Metacarnites*, mentioned below, and the family Tibetitidae is not now believed to indicate affinity, any more than *Pseudosirenites* Arthaber has anything to do with the real *Carnites*. The resemblance between the Ladinian *Rimkinites* and the Norian *Dittmarites* in the *Polyplectus*-ribbing is also taken to be merely accidental. But Diener's latest (1925) reference of *Carnites* to the family Noritidae, instead of the Hungaritidae, is equally untenable. The resemblance in suture-line is slight, for example, in the case of the monophylloid suture-lines of *Bosnites* and *Neoclypites* ; in the typical genera *Norites* and *Carnites* it is almost *nil.* Even externally they are scarcely comparable, and if there is any connection at all between *Carnites* and *Rimkinites*, then *Norites* cannot come into consideration. This brings us back to the Hungaritidae as the presumably nearest relations of *Rimkinites* and its derivative *Carnites.*

The genus *Pseudocarnites* Simionescu, 1913 (genotype : *P. arthaberi* Simionescu, 1913) was described by Diener (1915) as a natural development of *Carnites*, having proceeded even farther along the same direction of variation, i.e. having an additional adventitious saddle. We note, however, the absence in *Pseudocarnites* of the median keel, conspicuous in *Carnites* at small diameters, and the presence of monophyllic saddle-endings, and it could also be held that Simionescu was right in considering his genus as a pre-*Carnites* rather than a post-*Carnites* development. But the resemblance to *Procarnites* Arthaber, as already mentioned (see Part IV, p. 165), of *Carnites* as well as *Pseudocarnites*, cannot be upheld. The phylloid terminations of the saddles, while not supporting affinity of *Pseudocarnites* with the Pinacoceratidae, could be considered to have a certain parallel in *Klamathites* Smith ; but there is a striking difference from the suture-line of *Parahauerites* Diener.

The former genus, *Klamathites* J. P. Smith, 1927*a* (genotype : *K. schucherti* Smith, 1927), was included by its author in a family " Haueritidae " (of the Pinacoceratoidea), but obviously has nothing to do with the true *Hauerites*, discussed below (p. 71). The division of the external saddle is slight in the latter, although it is of much later date, whereas in *Klamathites*, the adventitious elements are so irregular as to defy attempts at unravelling their proper order. There is no median keel, as in *Carnites*, and the bicarinate venter becomes rounded off in the adult, without trace of lateral tuberculation. Since J. P. Smith's account of the relations of this genus is somewhat contradictory, it may suffice to add that he himself considered *Parahauerites* Diener, 1916*e* (genotype: *Hauerites ashleyi* Hyatt & Smith, 1905) to be a kindred genus. He, however, wrongly renamed it "*Fremontites*," eleven years after the creation of *Parahauerites*, stating that it differed from *Klamathites* merely in its short and little-developed adventitious series. Arthaber (1911) had stated that the Californian "*Hauerites*" did not belong to his heterogeneous assemblage attached to *Carnites*, but though *Parahauerites*, in its suture-line, resembles the true Norian *Hauerites* perhaps more than it does *Carnites*, it is not believed to be related to the former. The resemblance, in the suture-line, to *Paratibetites*, and even some Sirenitids which could be taken to be due to their common ancestry in the Trachyceratoid stock, has already been referred to.

Dieneria Hyatt & Smith, 1905 (genotype: *D. arthaberi* Hyatt & Smith, 1905) is tentatively inserted here, because it was stated to have a strong external resemblance to *Parahauerites ashleyi*. It differs in its "entire" suture-line, of course, and that alone prevents any closer comparison with Pinacoceratids which had a greatly complicated and convex suture-line, with adventitious elements already in pre-Carnian times. There is almost certainly no connection between *Dieneria* and certain similar Eotriassic genera, e.g. *Ambites* (Smith) or *Episageceras* and *Hedenstroemia* (Pompeckj). The Middle Triassic Noritidae and especially such specialized developments as *Arthaberites* or *Bosnites* are also probably quite unrelated, but the high external lobe, found in many bicarinate forms, is also seen in the young *Carnites*, in what Mojsisovics (1873) called the *Hungarites*-stage.

To the present family is also referred **Neoclypites** nom. nov., created for "*Metahedenstroemia*" ? *desertorum* Johnston (1941, p. 460, pl. 61, figs. 2–3) of Carnian age. Its author recognized that it might belong to a new genus, and questioned its reference to the Lower Triassic *Metahedenstroemia*, while at the same time stating that there was resemblance to another new Nevada species, *Perrinoceras novaditus*. This is referred to above, under Longobarditinae, as it is still close to the persisting Hungaritid root stock. I cannot see any connection between *Neoclypites* and the

Anisian genus *Arthaberites* which is here included in the family Noritidae (Part IV, p. 282).

M. Family PROTEUSITIDAE nov.

The genus *Proteusites* Hauer (1887) (misspelt *Proteites*[1] in Part IV, p. 108) is based on a peculiar Bosnian ammonite, *P. kellneri* Hauer (1887), which shows an unusual combination of characters. *Proteusites,* as its name implies, indeed seemed to be able to change its form at will. It has undoubted affinity with, and obviously the suture-line of, *Ceratites,* yet it has sufficient resemblance to Ptychitidae and to Gymnitidae to have been included with either by different authors. *Proteusites* baffled its own creator, who left some evident relations in the genus *Ceratites,* although Hauer mentioned that there was close affinity between these and what he considered the more typical forms. Then Waagen (1895) thought *Proteusites* represented a group of forms apparently most nearly related to *Acrochordiceras,* which was quite a shrewd guess, although it may not seem so immediately, or to *Stephanites.* Yet he included two of the species, *P. crasseplicatus* and *P. striatus,* left by Hauer in *Ceratites,* in the genus *Flemingites* Waagen, partly, no doubt, on account of the spiral lineation, another peculiarity of some of the forms. Diener (1897*a*) promptly rejected this assimilation, but two years previously he had discussed the resemblance of some of the Bosnian ammonites to the genus *Japonites* and had called *Proteusites* a completely isolated genus. In establishing for it a separate family, I am acknowledging the accuracy of Diener's pronouncement.

Haug (1894) classed *Proteusites* with *Parapopanoceras* and *Ptychites,* and though Diener had considered the resemblance to the last genus only superficial, J. P. Smith included *Proteusites* in the family Ptychitidae in his latest works (1927*a*, 1932), stating that the larval stage of *Pt. seebachi* Mojsisovics greatly resembled *Proteusites.* The fact, however, that he figured at the same time as *Proteusites rotundus* Smith a Meekoceratid from the Lower Trias of California (apparently a form near to *Preflorianites,* see Part IV, p. 131) shows that he cannot have known the true Bosnian *Proteusites,* except

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[1] The change from *Proteusites* Hauer to *Proteites* was made by Mojsisovics in 1893, but a *vox hybrida* is not an "evident error," in accordance with Rule 19, and thus cannot be changed.

from published illustrations. On the other hand, Smith did not improve the position by reviving (in 1932) his original grouping of *Proteusites* with the Celtitinae (1913), especially as this was done on the page following that on which he had described *Proteusites* as probably a Ptychitid.

Arthaber, in his revised classification of 1914, included some of the Bosnian ammonites in the genus *Japonites* and, therefore, in the sub-family Gymnitinae of his Ptychitidae. Mojsisovics, however, was probably right when, in 1902 (*a*), he listed *Proteusites* among the genera of the super-family Ceratitida. For the Meekoceratidae, as understood by him, included *Beyrichites;* and while this genus itself is no more than a distant cousin of *Proteusites*, it helps to explain why that genus has been confused with Gymnitids as well as Ptychitids. Diener discussed some of these Ceratitids in his well-known paper on the phenomena of homoeomorphy among Triassic ammonoidea (1905*a*).

The Ceratitid suture-line of *Proteusites* remains its most constant and most reliable feature. There are changes in ornamentation, two species even having umbilical tubercles, and the uncoiling body-chamber, up to a whole whorl in length, may vary considerably. But no subdivision is necessary for the present. Even before Kraus (1916) called *Proteusites* a typical Balkan element it had been described from as far afield as Kashmir ; and I agree with Diener (1913) that his *P. indicus* is a close ally of the genotype, *P. kellneri*. I accept Kraus's identification with *Proteusites* of Hauer's groups of *Ceratites crasseplicatus* as well as of *C. minuens* (= *C. "evolvens"*) and I am including here the species in which the serration has encroached on the tips of the saddles and on their sides, besides those in which the saddles are entire. That is to say, the suture-line may be faintly ammonitic, instead of ceratitic, as in *Beyrichites* and without in the least resembling the far more complex suture-lines of *Ptychites* or *Gymnites*.

It is true that *Proteusites* has globose young and constrictions like inner whorls of *Ptychites;* the latter also does not commonly show uncoiling outer whorls, and umbilical tubercles are unknown in *Ptychites*. But looking at the suture-line of a form like *Ptychites* (*Arcestes* ?) *globus* Hauer, with its narrow-stemmed median saddle in the external lobe, we notice a fundamental difference in the two stocks. It was only when I broke up young *Ptychites* to study the development of the suture-line that I realized its general resemblance to that of Arcestids and obvious difference from the probable development of the ceratitic suture-line of *Proteusites*. Unfortunately there is not the almost unlimited quantity of material[1] for dissection as in *Ptychites*, but one section of a young *Proteusites labiatus* Hauer shows little difference from similar sections of *Ptychites*, with external siphuncle. But in *Paraceratites* (*P*. cf. *lenis* Hauer sp.) the siphuncle is also external, though the whorls are higher and there are no constrictions.

N. Family APLOCOCERATIDAE nov.

There were two genera of Ceratitid affinities which I had great difficulty in placing when the genera of the Ceratitida were reviewed in 1934. One of these was the genus *Apleuroceras* Hyatt (1900), attached by him to the Lower Triassic family Meekoceratidae, but of Ladinian age. That genus was based on the very rare *Ceratites sturi* Mojsisovics, representing the group of the "*Ceratites nudi*." Unfortunately this was quite misunderstood by Waagen (1895), who included in it two Lower Triassic species from the Salt Range and so misled Hyatt, the creator of the genus *Apleuroceras*.

Philippi (1901) rejected the group of *Ceratites nudi* and correctly pointed out that it was altogether improbable that the two doubtful Salt Range species, described by Waagen (1895) and referred to this group, had any connection with *Ceratites*. Judging by their associates, it seems probable that Waagen's *Ceratites wynnei* (1895, p. 50, pl. xi, fig. 5) and *C. patella* (*ibid*., p. 51, pl. iv, fig. 2) are Prionitids or Sibiritids, and the latter species, at any rate, was already included by v. Krafft (in v. Krafft & Diener, 1909, p. 130) in *Sibirites*, although it is quite different from what has been described (Part IV, p. 343) as *Sibirites* s.s.

The second genus was *Aplococeras* Hyatt (1900), which was created for *Dinarites avisianus* Mojsisovics, a species as common in certain Ladinian beds (e.g. the Forno Limestone) as *Apleuroceras sturi* is rare. Now Mojsisovics, after first (1878) attaching *Aplococeras avisianum* to the genus *Trachyceras*, referred it to *Dinarites* in 1882, and four years later to the group of spiniplicate Dinaritids (see *Olenikites*, Part IV, p. 360). He was, in fact, surprised to meet this Arctic group

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[1] The Collection includes about 100 specimens of *Proteusites* from Stavljan, Volujak Mtn., Bosnia, and the Mali Durmitor Mts., Montenegro.

again in the Ladinian and Carnian beds of the Mediterranean Province, with "*Dinarites*" *avisianus*, "*D.*" *doelteri*, and "*D.*" *eduardi*. The resemblance, however, is not very close; and, in my opinion, *Aplococeras* has no direct connection with the Lower Triassic Dinaritids.

Hyatt thus misinterpreted *Aplococeras* as he had misunderstood *Ceratites sturi*, and he included his genus in the entirely distinct family Prionitidae, again together with a number of unrelated Eotriassic genera. Hyatt & Smith (1905) and J. P. Smith (1914) then rejected *Aplococeras* altogether, and included the *avisianus*-group again in the genus *Dinarites*, as did Diener in 1915(*a*) and 1925.

The two groups are now united in one family (named after the common *Aplococeras*) because Mojsisovics thought *Ceratites sturi* was in all probability related to *Aplococeras misanii*, differing only in being thicker, less evolute, and in having a slightly more complex suture-line, with serrated lobes. At the same time Mojsisovics stated that the ancestors of *Ceratites sturi* were not to be looked for among the *Ceratites* of the Muschelkalk, but among the Dinaritids which, according to him, persisted into the Carnian. These late "*Dinarites,*" of course, are the *avisianus*-group or the genus *Aplococeras*.

As Mojsisovics pointed out, the genus *Ceratites* in the wider sense is chiefly Anisian, becomes rare in the Ladinian and has only one representative left in the Upper Ladinian, namely, *C. sturi*, the genotype of *Apleuroceras*. The almost complete loss of ornamentation gives it an unusual aspect, but the resemblance to the equally plain *Dinarites mohamedanus* (see Part IV, p. 387) is undoubtedly accidental, in view of their wide separation in time. Hyatt was thus well justified in giving this degenerate end-form a distinct generic name.

The genus *Aplococeras* Hyatt, on the other hand (genotype: *Dinarites avisianus* Mojsisovics, 1882), was stated to resemble the Eotriassic *Xenodiscus* and *Ophiceras*, and thus seemed out of place in the Upper Ladinian and Carnian. Here again the resemblance is only general, for these early Triassic ammonites developed their own specialized types whereas the Aplococeratidae are interpreted as Ceratitids with simplifying suture-lines and a tendency to lose their ornamentation. The smooth, *Lecanites*-like *A. eduardi* Mojsisovics, it is true, has been claimed as leading to the Trachyceratid *Klipsteinia*. The relationship, however, is probably not so close as appears; and, after all, the Trachyceratida on the whole are derivatives of the Ceratitida. A certain resemblance is thus to be expected in these more or less smooth offshoots.

A. avisianum occurs in such numbers that Bubnoff (1921) was tempted to study its variability by statistical methods. The material does not seem to me especially suitable for such a study ; for, apart from the possibility that forms of several geological horizons became incorporated in this condensed deposit, made up entirely of shells of what appears to be one species, the preservation in a saccharoidal, white limestone is not very favourable. It may suffice to mention that Bubnoff's observations on the suture-line still leave it as incompletely known as when Mojsisovics described it ; and the siphuncle and siphonal funnels could not be observed with certainty. The result of so much labour, then, was to demonstrate that on the whole the ammonites tend to compensate a decrease in the number of ribs by an increase in their strength, so that the species "*Dinarites*" *doelteri* falls within the limits of variability of *A. avisianum.* This was recognized by Salomon (1895), many years before, from a mere inspection of the specimens.

Bubnoff, however, discovered that *A. avisianum* has constrictions on the first two whorls, before the successive phases of ornamentation are developed. These may show that *Aplococeras* has nothing to do with the Eotriassic genera above mentioned, but the ribs and umbilical bulges are very similar to the ornamentation of "*Lecanites*" *vogdesi* Hyatt & Smith, and, as J. P. Smith himself noted (1914), that of his "*Dinarites*" *desertorus.* The former has an entire suture-line, the latter has ceratitic lobes. In the specimens of *A. avisianum* before me, the entire saddles can be seen, but it remains uncertain whether the lobes are denticulated, as in *A. eduardi,* or entire as in Smith's "*Lecanites.*"

A number of species of this American group of forms are represented in the Collection,[1] including some examples of "*Lecanites*" *parvus* from Prof. Smith's own collection. One of these was sectioned, together with other apparently co-specific examples from the Train collection, and they all showed a siphuncle that is external from the start, as in *Ceratites.* The thickness of the siphuncle, however, is greater ; it may be as much as a third of the whorl-diameter in the third whorl, and still a quarter in the fourth. The actual

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[1] Many examples in the P. Train Collection from Nevada are still unsorted and unnamed.

diameter is about ·2 mm., as in the Tropitids, whereas in the few Ceratitids sectioned it is only about one-fifth to one-sixth of the whorl-height, or approximately ·15 mm. The protoconch is of medium size (·35–·4 mm.), again as in the *Ceratites*. The septation is very irregular, and there may be unusual approximation of the final septa. For example, one section shows no fewer that 15 septa on the last chambered half-whorl, at 20 mm. diameter (the other half being broken); but the polygyral earlier whorls have 14, 12, 11, 9, 8, and 7 erratically-spaced septa. Another slide shows 20 septa on the last whorl, followed by only 10 on the next inner volution, equally irregularly spaced. Unfortunately not nearly enough observations are available, to date, to appraise any possible phylogenetic significance of such irregularities, as distinct from mere individual growth phenomena.

At small diameters, these Nevada specimens are indeed much like the Carnian true *Lecanites*, perhaps slightly more evolute than *L. glaucus* itself. But at 27 mm. diameter they are quite different; for the shell then has a slightly crenulate and distinctly narrowed periphery. This is reminiscent of the ventral aspect of *Xenoceltites subevolutus* Spath, but the striation is rursiradiate, not prorsoradiate (see Part IV, pl. viii, fig. 2). "*Lecanites*" *vogdesi*, according to two body-chamber examples of not quite 30 mm. diameter, from the J. P. Smith collection and many Nevada duplicates, has strong and apparently very variable ribbing, an anguliradiate rib-curve, and a venter that again tends to become narrow, without, however, showing a ventro-lateral edge, or a flattening. The exaggerated ornamentation of "*L.*" *crassus* Smith is essentially the same as that of "*L.*" *vogdesi*, so that the four Nevada species are closely similar.

Smith described his "*Lecanites*" as progressive, radical types, so they should be unconnected with the distantly similar "*Xenodiscus*" *multicameratus* and "*X.*" *bittneri* of the "*Parapopanoceras*" beds of California. These have a ceratitic suture-line and prorsoradiate ribbing like *Xenoceltites*; in fact, *X. bittneri* has already been described (Part IV, p. 126) as probably a late form of *Xenoceltites*. The decline of the ornamentation in "*Lecanites*" *vogdesi*, moreover, has a parallel in the slightly less evolute *Ceratites weaveri* Smith, which may be a contemporary of these Anisian "*Lecanites*," but already resembles *Aplococeras*. Smith's dwarf species was described as the most atavistic form of *Ceratites* in the fauna of Nevada. The view that it was probably "reversionary or retarded" was, however, negatived by the statement that it might equally well be a primitive form, little modified from the ancestral type, i.e. the parent *Meekoceras*.

It seems to me more probable that the group just discussed is a suturally reduced offshoot of the contemporary *Ceratites*, for which a new name: **Pseudaplococeras** gen. nov. (genotype: "*Lecanites*" *vogdesi* Hyatt & Smith, 1905, p. 139, pl. lx, figs. 12–15) may be suggested. The more strongly ornamented "*Dinarites*" of the same beds do not show the peculiar rursiradiate ribbing of the forms of "*Lecanites*," and the contracting or narrowing periphery; but being very rare, it might not be considered necessary to separate them also with a new name, just because their lobes are ceratitic. This would be expected in a stock derived from the persisting *Ceratites* and represents merely a stage in the development of the smooth "*Lecanites*," with goniatitic suture-line. Nevertheless, since the genus *Velebites* Salopek, 1918*b* (genotype: *V. dinaricus* Salopek, 1918*b*) was introduced (originally as a subgenus of "*Dinarites*") for a form with ceratitic suture-line which differs only slightly from *Aplococeras* (significantly in the more re-curved ribbing), so we may re-name the last unplaced "*Dinarites*." The name **Metadinarites** gen. nov. (genotype: *Dinarites desertorus* J. P. Smith, 1914, p. 69, pl. lxxxix figs. 3–4) is therefore here proposed.

Finally, there is the Carnian "*Dinarites*" *electrae* Renz (1911), which was considered a late offshoot of the Dinaritid stock, like *Aplococeras eduardi* Mojsisovics. It is possible that the latter species suggested to Renz that the group of *A. avisianum* was intermediate between *Dinarites* and *Arpadites*; in any case, the resemblance between the typical *Aplococeras* and the Greek species seems equally remote. I am not at all satisfied that "*Dinarites*" *electrae* has been correctly interpreted, but since the somewhat crude drawing may be partly responsible for its peculiar appearance, re-examination of the type by a specialist will have to be awaited. If the species belongs to the present family at all, it cannot be accommodated in any of the genera above discussed.

The genus *Dobrogeites* Kittl, 1908 (genotype: *D. tirolitiformis* Kittl, 1908), as the name of its only species implies, resembles *Tirolites* in ornamentation, but it differs in suture-line. *Meekoceras* seemed to Kittl to offer more analogy as regards the latter character, but as it differed in most other features, *Dobrogeites* appeared to occupy an isolated position. Its inclusion in Meekoceratidae in Zittel's Grundzüge (1924) is therefore no more helpful, and it is necessary to find a more likely relationship.

There are four examples known of this unusual genus, and they appeared to Kittl to have a juvenile aspect. Yet for ammonites of so minute a size, they show a remarkably complete range of characters, from whorl-shape and ornamentation, even of the inner whorls, to the suture-line, all at a stage at which other ammonites are often almost featureless. The genus is also known to be Anisian in age, so it should not prove impossible to find a family in which to accommodate it. Unfortunately those groups that most resemble *Dobrogeites* in external shape, especially the flattened divergent whorl-sides and broadly arched periphery, or in the serial suture-line, are leiostracous, i.e. unornamented stocks, while trachyostracous families like Tropitidae or the Celtitidae, with long body-chambers, have a characteristic, large lateral lobe which does not fit in at all with the suture-line of *Dobrogeites*.

The Indian *Sibirites prahlada* Diener (1895*b*), which in Part IV (page 359) I doubtfully included in the genus *Durgaites*, has Tirolitid inner whorls, like *Dobrogeites*, but whorl-shape and peripheral ribbing are quite different. There is more agreement in the suture-line which has entire saddles, and the external saddle is the largest, as in *Dobrogeites*, but there are only two lateral lobes and no auxiliaries. There is nothing known so far to connect *Dobrogeites*, as a specialized or degenerate end-form, with the early Ceratitida.

Among later types, only the "*Dinarites*," above referred to as *Metadinarites*, and the associated *Pseudaplococeras* could be compared to *Dobrogeites*. "*Dinarites*" *desertorus* Smith (1914, pl. lxxxix, figs. 3–7 ; pl. xcviii, figs. 13–18) has too rounded a whorl-shape and is too evolute to be a close relation, but the Ceratitid stock from which it sprang may account for the *Tirolites*-like inner whorls of *Dobrogeites*. The suture-line, with its large external saddle, requires only a few more similar saddles to resemble the suture-line of *Dobrogeites*. "*Dinarites*" *pygmæus* Smith (1914, pl. lxxxix, figs. 8, 9) again, has convergent instead of divergent whorl-sides and looks so different from the small *Dobrogeites* only because it is so much larger. The tendency of a ceratitic suture-line to become serial, i.e. to increase the number of elements instead of the complexity of the saddles is seen in some Hungaritids to be probably correlated with the flattening of the whorl-sides. Kittl has shown the increase in the number of saddles in *Dobrogeites* to be rapid and the suture-line may well have been at first a normal ceratitic suture-line.

The inclusion of *Dobrogeites* in the family Aplococeratidae can only be provisional, for direct connection cannot be demonstrated, and distant affinity is suggested chiefly because none of the other families of Triassic ammonites here dealt with offers a likely alternative. For example, the Anisian forms described under such erroneous names as "*Xenodiscus*" and "*Xenaspis*" all lack the characteristic *Tirolites* ornamentation and seem less probable relations, while disagreeing at least as much in the suture-line as the Aplococeratidae.

VI. Super-family TRACHYCERATIDA, Haug, 1894 (emend).

Most authors are agreed that the Trachyceratids are descendants of the Ceratitids in the wider sense, but there is little connection between the classification here adopted and that first proposed by Mojsisovics in 1893, and expounded by Haug in 1894. For while separation of the present division from the super-family Ceratitida is a matter of expediency in view of the large numbers of smaller units involved, their division into descendants of Dinaritinae and Tirolitinae respectively seems to me entirely impracticable. These two Eotriassic groups, already dealt with as separate families in Part IV, disappeared completely before the Anisian ; and Mojsisovics, indeed, considered *Balatonites* (see p. 15), a much more highly specialized Ceratitid, to be the root of *Trachyceras*, connecting it with *Tirolites*. Haug thought that nothing seemed less demonstrated than this affiliation, but went on to say that the Anisian *Balatonites* was succeeded, soon after, by *Anolcites* Mojsisovics, then, in the Lower Ladinian, by *Trachyceras* and *Protrachyceras*.[1] The genus *Nevadites* Smith was then unknown. Its suture-line is still

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[1] According to Mojsisovics (1893) *Protrachyceras* ranged from the Lower Ladinian (and possibly Anisian) up into the Carnian, where it persisted, with a few species, as contemporary of its derivative, *Trachyceras*. Both became extinct in the Middle Carnian.

ceratitic, with the full number of elements, its body-chamber occupies half a whorl, and while aptly described as a primitive *Anolcites*, its resemblance to the contemporary *Frechites*, *Kellnerites* and similar Ceratitids is striking. All the same none of the ornamented Ceratitids can be the immediate ancestor of Trachyceratids.

J. P. Smith (1914) included in the true Trachyceratids, apart from the four genera already mentioned, the genus *Sirenites* Mojsisovics, but he dealt only with the American forms which at that time apparently did not include representatives of the Upper Ladinian and Lower and Middle Carnian stages, including the Trachyceratan age (Part IV, p. 39). On the other hand, Smith excluded *Clionites* (which had been subdivided into five subgenera by Hyatt & Smith in 1905), and in 1927*a* he kept this distinct from *Arpadites*, of which genus *Clionites* had been considered a subgenus by Mojsisovics. The family Arpaditidae Hyatt (1900) was accepted by J. P. Smith (in Zittel, 1913), but *Clionites* (omitted in Hyatt) was then unexpectedly referred to Trachyceratidae. The family Clionitidae is then used here for convenience, but it is far more restricted than what Arabu (1932) called a family (" groupe modifié "), his Clionitidae and Ceratitidae corresponding more or less to Arthaber's two families, Trachyceratidae and Ceratitidae.

Most of the existing subdivisions, such as the families Arpaditidae, Heraclitidae, etc., many of them dating from 1900, are adopted, some with modifications suggested by a study of the material in the Collection from the classical Alpine localities as well as from India, Timor, Nevada and California. There are many Trachyceratida in the Klipstein Collection, acquired in 1851, and containing those specimens in his own possession that were figured in the famous ' Beiträge zur geologischen Kenntniss der Östlichen Alpen ' (1843). As the ' History of the Collections contained in the Natural History Departments of the British Museum ' (Vol. I, 1904, p. 303) states, " other series of Klipstein's collecting were to be seen at Budapest and elsewhere, but that in the British Museum was the one by which Klipstein's work must be interpreted."

Klipstein's work has been revised, chiefly by Laube and Mojsisovics ; and I have not sufficient or larger material to question their identifications. Moreover, Klipstein's species, many established on quite insufficient grounds, are often represented by a number of differing specimens. It must be left to future investigators of the St. Cassian fauna to re-examine those of Klipstein's species which are still unrecognized.

In view of the importance attached by some authors to the characters of the inner whorls as displayed in thin median sections, it is a matter for regret that so few Trachyceratids have yet been examined. Branco (1879) figured inner whorls of *Trachyceras* cf. *münsteri* (Wissman) Münster sp. and *Sirenites pamphagus* (v. Dittmar), showing an external siphuncle, but sections of *S. agriodus* (v. Dittmar), published by Schindewolf (1934) and prepared by myself, prove that the siphuncle does not become external until a diameter of 2·5 mm. is reached. The siphuncle is fairly thick (about one-fifth of the height in the third whorl) and the protoconch is moderately large (·4–·45 mm.). Again, sections of *Trachyceras* aff. *aon* (Münster) and a *Klipsteinia* sp. show a siphuncle that remains away from the venter throughout the septate stage, though it is sometimes difficult to be certain that the funnels are not really external. On the other hand, in one of the Californian forms of the group of *Traskites fairbanksi* (Hyatt & Smith) there can be no doubt about the position of the siphuncle, well below the grooved venter. The siphonal funnels can be seen to the last septum, at 13 mm. diameter ; they are directed forwards and not external throughout. There are 15 septa on the last whorl (the final 12 of them approximating), and 9 and 10 on the innermost two whorls. In *Trachyceras* aff. *aon* the last chambered whorl has 17 septa, followed by 9 and 10 on the two inner whorls. But since the section of *Sirenites agriodus* before me has 17 septa on the last chambered whorl (at 5 mm. diameter), with 13 before that, and more numerous septa than Schindewolf's section on the innermost volutions, there is probably no significance in the actual number. The spacing seems irregular in all. The protoconch in *Traskites* (·3 mm.) is smaller than that of the other Trachyceratids so far discussed.

Five Nevada examples of *Anolcites* (group of *A. meeki* Mojsisovics) and five of *Nevadites* (group of *N. whitneyi* Gabb sp.) were sectioned, but the coarsely crystalline matrix had displaced or destroyed most of the finer detail, such as the siphonal funnels or even the septa. Both genera show a slower increase in whorl-height than *Trachyceras*, *Sirenites* or *Drepanites*, but the siphuncle, in *Nevadites* at least, also is not quite external in the third whorl and still slightly away from the periphery at the end of the septate stage (at 12–13 mm. diameter in two specimens). *Anolcites* has 18 septa in the first two whorls, as in *Sirenites* (Schindewolf, 1931) and 17 in another example, but the funnels are not preserved.

A. Family TRACHYCERATIDAE Haug (1894).

The family Trachyceratidae is still ascribed to Mojsisovics, e.g. by Diener (1925), but the "tribes" recognized by the former in his sub-family Tirolitinae (later [1896*a*] family Tirolitidae), were first spoken of as families by Haug. Hyatt (1900) may or may not have adopted the family Trachyceratidae from Haug, but J. P. Smith (1913) reduced this to a sub-family (of Ceratitinae) and in 1927*a* abandoned even this, including *Trachyceras*, *Clionites* and various other genera merely in the family Ceratitidae. Arthaber (1914) objected to this, but Smith does not appear to have seen Arthaber's work, since he only referred to the paper of 1911.

The family is based on the genus *Trachyceras* Laube, 1869 (genotype: *T. aon* Münster sp., 1834), and the genus *Paratrachyceras* Arthaber, 1914 (genotype: *P. hofmanni* Böckh sp., 1873) is a close ally. It was created for the forms with little or almost no tuberculation. Some, but not all, of the species of *Trachyceras* and *Protrachyceras*, listed by Arthaber as belonging to *Paratrachyceras*, may be properly included here; decidedly not *Anolcites richthofeni* Mojsisovics, which may well have been correctly interpreted by its author.

A species of *Paratrachyceras*, scarcely differing from the genotype, *P. hofmanni*, except in its slightly wider umbilicus is *P. meginae* (McLearn).[1] Its author established for it the sub-genus *Meginoceras* (of *Steinmannites*), but later included it correctly in *Paratrachyceras*,[2] while quoting it in 1937*a*, *b*, and 1940*b* as "*Sirenites*" *meginae*. The Collection includes examples of this species as well as of *Isculites schooleri*, *Protrachyceras sikanianum*, *Silenticeras hatae* (see p. 59), *Lobites paceanus* McLearn, and the species of *Nathorstites*, listed in 1940, so that the Carnian age of the *Nathorstites* fauna of the Schooler Creek Formation (British Columbia) seems doubtful. *Paraceratites hofmanni* is claimed as Middle Carnian by

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[1] There is a possibility that this species is closer to *Trachyceras* (*Protrachyceras*) *homfrayi* (Gabb) than the mediocre illustration. copied in Smith (1914), suggests.

[2] Stamped correction in separates of above.

Arthaber, but McLearn suggested a Ladinian or very early Carnian age for this *Nathorstites* fauna, and he may have been right in putting it as low as Ladinian. The American *P. homfrayi* (Gabb) is also of that age.

Another close ally of *Trachyceras* is *Protrachyceras* Mojsisovics (1893), connected with the former by transitions, if the arrangement of the peripheral tubercles is considered a primary distinguishing feature. Unfortunately the selection of a genotype of *Protrachyceras* has not yet been settled, so far as I know. As Hyatt & Smith (1905) mention, the first species listed by Mojsisovics is *P. chiesense,* from the Ladinian Buchenstein Beds, and since Mojsisovics expressly described this as the apparent starting-point of one series of Trachycerata, it might be considered a suitable species to select as genotype ; for the fact that it is based on a fragmentary example is irrelevant. Hyatt & Smith considered *P. rudolphi,* the first species described by Mojsisovics in 1893, to be a better genotype, if not so desirable as the well-known *P. archelaus* (Laube), and I agree, since even Arthaber figured an example of this species as a member of the subgenus *Protrachyceras.*

It has yet to be shown that the early *P. chiesense* gave rise to the presumably more representative forms of *Protrachyceras* of the *archelaus* zone (Upper Ladinian), but it may be noted that " *Trachyceras* " *armatum* which was at first taken to be a near relation of "*T.*" *chiesense,* was transferred to "*Anolcites*" by Mojsisovics in 1893, without, however, fitting into that genus any more than into *Protrachyceras* (see p. 50).

The last genus is connected by transitions with *Nevadites* Smith, 1914 (genotype : *N. merriami* Smith), such as the *Protrachyceras* sp. ind. figured by Diener (1900*a*) or *Ceratites ecarinatus* Hauer, which were considered Anisian forerunners of *Protrachyceras* by Kraus (1916). There are also transitions from that genus to *Anolcites* Mojsisovics, 1893 (genotype : *Trachyceras doleriticum* Mojsisovics, 1882). The typical species of *Anolcites,* from *A. doleriticus* to *A. richthofeni* and the more tuberculate *A. amicus* (Mojsisovics), in fact are rather distinct from some of the Nevada forms that might almost be referred to *Nevadites.* For instance, of two examples of *Nevadites* (*Anolcites*) *humboldtensis,* labelled thus by Prof. Smith himself, one of 38 mm. diameter is an *Anolcites,* comparable to *A. gabbi* Smith, but at 53 mm. the prominent lateral tubercles of *Nevadites* have appeared.

Nevadites and *Anolcites* have been recorded by Jaworski (1922) from Peru. It has already been mentioned (Part IV, p. 37) that these Middle Triassic genera were misidentified. Steinmann's original determinations of these ammonites as *Metasibirites*, etc., even if open to criticism specifically, were much less wide of the mark. Anyhow, they did not require a highly improbable assumption as to how these Middle Triassic genera became incorporated in a Norian fauna.

The Sirenitids are a large group of Upper Triassic Trachyceratidae, but they are not derived from just one branch, say the genus *Protrachyceras*, so that they are not separable as an independent family. The typical genus *Sirenites* Mojsisovics, 1893 (genotype: *S. senticosus* Dittmar sp., 1866) is characterized by the doubling of the outer tubercles taking place by bifurcation, not as in *Trachyceras*, by doubling on the same rib. There are thus five rows of tubercles or delicate spines, arranged in spiral lines. Those accompanying the siphonal furrow are often fused into discontinuous, ropy keels, and with those of the ventro-lateral edge are rather more prominent than the two lateral or the umbilical rows of spines. *Sirenites* is closely related to the more compressed species of *Protrachyceras*, with a varying number of rows of spines, e.g. the Himalayan *P. ralphuanum* Mojsisovics. The ribbing is equally elegant, and neatly sigmoidal, but the ribs bifurcate at the tubercles on the ventro-lateral edges, and become strongly projected, to produce the tubercles at the border of the siphonal furrow. These bordering tubercles are often united, as mentioned, but in *Anasirenites* Mojsisovics, 1893 (genotype: *A. ekkehardi* Mojsisovics, 1893) they develop into continuous keels, more prominent than in Arpaditidae, which, however, may otherwise be quite different.

The suture line in *Sirenites* is ceratitic or dolichophyllic, i.e. ammonitic but not deeply indented, as in *Trachyceras*. There is a tendency to the formation of adventitious elements from the external saddle which, when fully developed, leads to *Pseudosirenites*, mentioned below.

Diplosirenites Mojsisovics, 1893 (genotype: *D. raineri* Mojsisovics, 1893) was said to differ in having double tubercles at the siphonal end of the ribs, thus presenting the *Trachyceras* type of ornamentation, as distinct from the *Protrachyceras* type in *Sirenites* s.s. There are transitional specimens in which it is not easy to tell whether they are still *Protrachyceras* or already *Sirenites*, but it is almost impossible to be certain that the outer tubercles are either single or double, unless the specimens are perfectly preserved. *Anasirenites* and *Diplosirenites* were originally introduced as sub-genera of *Sirenites* and they were still quoted as such by Kutassy (1933), but Hyatt listed them as independent genera as long ago as 1900.[1] If sub-genera are desirable in any genus, they are in *Sirenites.*

Diener's *Sandlingites pearsoni* (1906*a*) from the *Tropites* Limestone of Byans, does not seem to differ much from the associated Sirenitids, but the genotype of *Sandlingites* has a rather wide ventral area and inner tubercles. This genus is now included in Clydonitidae (see p. 48).

Another genus included here is *Welterites* Diener, 1923 (genotype: *W. egregius* Diener, 1923). It was probably correctly compared to the Sirenitids, especially in view of the agreement in suture-lines. *Vredenburgites* Diener, 1916*e* (genotype: *Sirenites vredenburgi* Diener, 1906*a*) is another closely allied genus. The ornamentation of its almost involute shells has a curious resemblance to that of certain fragments of large body-chambers of *Eutomoceras* in the Collection (compare Smith, 1914, pl. xc, fig. 1), but, of course, the siphonal channel is characteristic.

The genus *Pseudosirenites* Arthaber (1911) was considered a synonym of *Sirenites* by Diener (1915*a*), but a few of the species quoted by Arthaber may well be separated. As lectotype may be chosen *P. stachei* Mojsisovics sp. (1893), which is better known than *P. evae* of the same author, cited in the first place by Arthaber. For it shows the suture-line with its two adventitious elements, but otherwise not strikingly different from that of the typical Sirenitids and only vaguely resembling that of *Carnites.*

The genus *Dawsonites* J. Böhm, 1903 (genotype: *Trachyceras canadense* Whiteaves, 1889) was established presumably because its suture-line had entire saddles, but it may well be considered to be an independent offshoot of *Anolcites* (with ceratitic suture-line) distinct from *Protrachyceras.* J. P. Smith (1927*a*) relegated it as a sub-genus to *Clionites,* and thought it was perhaps identical with his own *Shastites,* but I can see no resemblance between the type of this sub-genus and the more involute Arctic *Dawsonites,* not even in the

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[1] The jumble of genera, including *Sandlingites* and other Trachyceratidae, together with Haloritidae, at the end of the family Tropitidae in Broili's revision of Zittel's 'Grundzüge' (1921, p. 547), reveals a deplorable lack of understanding of the systematic position of these genera.

suture-line. Böhm's view is therefore here accepted, and with its twelve rows of tubercles and its comparatively small umbilicus, *Dawsonites* is considered not a Clionitid, but a Trachyceratid. Its occurrence in British Columbia, Alaska and on Bear Island is no longer surprising, since comparable ammonite faunas are now known also from Eureka Sound, on Ellesmere Land (with *Trachyceras*), and from the New Siberian Island of Kotelny. That is to say, there is no reason for separating *Dawsonites* from *Trachyceras* merely because it is associated with the boreal *Nathorstites*.

The trachyceratoid ornamentation of *Dawsonites* may be held to have smaller systematic value than the suture-line. This has rounded, entire saddles, that might even be compared to those of immature *Amm. brotheus* Münster, in the Klipstein Collection, considered by Mojsisovics to be the young of the genotype of *Trachyceras*, i.e. *T. aon*. In *Dawsonites* the saddles remain entire. This does not affect the validity of the suture-line as the most reliable and generally the most stable character for classification.

The Trachyceratidae, considered by many to be the most attractive and perhaps the most characteristic of all Triassic ammonoids, next to the *Ceratites*, are well represented in the Collection, especially by many fine specimens from the world-famous Austrian localities, including some from Mojsisovics's own collection. There are also a few from other localities, notably Asia Minor and the Himalayas, British Columbia and California. In the Klipstein Collection there are probably all the "twenty aons" of which he was said to be the author. Laube reduced these and the earlier species of Münster to a comparatively small number, but Mojsisovics revived some. Since there are various discrepancies it may be advisable to record those of Klipstein's forms that have been recognized; most of them have already been listed in Crick's Catalogue (1898). It is obviously impossible, without having access at least to Laube's and Mojsisovics's material, to engage in a revision of the genus *Trachyceras* on the basis of the Klipstein Collection alone. So I am not attempting to express any opinion on many of these "species," often very small or defective.

As regards the group of *Trachyceras aon* (Münster), the genotype, the following Klipstein species, listed in the synonymy by Laube, are in the Collection: *Amm. humboldtii*, *Amm. spinulo-costatus*, *Amm. dechenii*, *Amm. credneri*, *Amm.*

noduloso-costatus, Ceratites zeuschneri, Goniatites ornatus. All these include the figured examples and, in some, a varying number of co-types, but in the case of *C. zeuschneri* the holotype has not been recognized, only an example from which the suture-line was taken. To these should be added *Amm. nodo-costatus,* which was also listed in the synonymy of *Trachyceras brotheus* (Münster), and *Ceratites brevicostatus,* which was also described as a separate species of *Trachyceras* by Laube.

Four of Klipstein's species, namely *Amm. ? mirabilis, Amm. veltheimii, Amm. ? larva,* and *Amm. armato-cingulatus,* were included by Laube in the synonymy of *Trachyceras brotheus* (Münster) but this form was itself considered a synonym of *T. aon* by Mojsisovics, together with *Ceratites meriani* Klipstein, and *C. münsteri* (Wissmann) Münster. The holotypes of all these five Klipstein species are in the Collection, as is that of *Ceratites ? jaegeri* which was listed as a synonym of *Trachyceras dichotomum* (Münster) by Laube, but treated as a separate form of *Trachyceras* by Mojsisovics, and included in *Paratrachyceras* by Arthaber.

Another four of Klipstein's species were considered by Laube to be synonymous with *Ceratites busiris* Münster, namely *Amm. bidenticulatus, Ceratites karstenii, C. agassizii,* and *Goniatites rosthornii.* There are fourteen examples of the last, but apparently not the figured specimen, while *C. agassizii* is not represented at all in the Klipstein Collection, or at least is not marked. Mojsisovics described *C. busiris* Münster as a *Trachyceras* in 1882, a *Protrachyceras* in 1893, and Arthaber (1914) made it a *Paratrachyceras* ; yet Crick already had described *G. rosthornii* as " *Klipsteinia boetus* (Münster) " ; *C. agassizii* was stated by Klipstein to be easily confused with *G. rosthornii ; C. karstenii* is referred to below as a *Klipsteinia* ; and *Amm. bidenticulatus* is also mentioned (p. 59) as being identical with *Protrachyceras basileus* (Münster) Mojsisovics.

The following five Klipstein species were treated as separate forms of *Trachyceras* : *Amm. ? mandelslohii, Amm. bouéi, Amm. subdenticulatus, Ceratites infundibuliformis,* and *Amm. aequinodus.* The holotype of the last, however, was stated to be in the Bronn Collection and the species is not represented in the Klipstein Collection. *Amm. subdenticulatus* was identified by Crick with *Trachyceras bipunctatum* (Münster), but Mojsisovics had them both as separate species and

Arthaber included *T. bipunctatum* in *Paratrachyceras*. On the other hand, *Amm.* ? *acuto-costatus* Klipstein, with four examples, including the holotype, and described as *Trachyceras* in Mojsisovics (1882), was referred by Welter (1915) to *Clionites*. The Timor form, however (represented by No. C. 40620), which the latter author identified with Klipstein's species, was included by Diener (1923, 1925) in Mojsisovics's *C. catharinae*. Klipstein's type is rather too small for more than generic recognition (diameter = about 11 mm.) and the ventral tubercles are as yet scarcely indicated.

In addition to these 26 Trachyceratids in the Klipstein Collection, there are examples of most of Münster's species, described in 1834 and 1841 ; and though these may not be of historic interest, they will show at least to future revisers of the St. Cassian fauna how Klipstein interpreted Münster's species and why he separated from them his own new species.

Many ammonites of the St. Cassian fauna, in the Klipstein as well as other collections, in the Museum have not yet been named. The American forms, also as yet unnamed, include only forms of the *Trachyceras* beds of Hyatt & Smith, not of the true Lower Carnian *aon* fauna, only lately (1941) made known by Johnston. There are, however, many Middle Triassic Trachyceratids from Nevada and Bosnia and Montenegro.

B. Family CLYDONITIDAE Mojsisovics (1879*a*).

This family, one of the original families established by Mojsisovics, must stand or fall by its typical genus *Clydonites* Hauer, 1860 (type : *C. decoratus* Hauer sp., 1846*a*). It was defined as evolute, with whorls covered with closely spaced, irregularly granular ribs, joining up across the periphery. Suture-line entire, wavy, with a high external saddle followed by a low lateral saddle. *C. modicus* (Dittmar), mentioned as a possible second species, was later referred to the genus "*Polycyclus*." As interpreted in 1893, *Clydonites decoratus*, of Norian age, is shown to be a finely ribbed, *Sandlingites*-like form, and though some species, like *C. goethei* of Mojsisovics's second group of *laevecostati* are more involute, Mojsisovics himself thought it possible that both genera developed in different directions from a common root. The agreement in suture-line is almost perfect. The genotype of *Sandlingites* Mojsisovics (1893), namely *S. oribasus* (Dittmar, 1866) has a comparatively wide periphery and umbilical tubercles. The description of *Sandlingites* as consisting entirely of dwarf-forms, probably degenerates (Hyatt & Smith, 1905), is not now very apt ; a Timor example of *Sandlingites archibaldi* Mojsisovics in the Collection has a diameter of 58 mm. Moreover, *Anolcites*, described as the undoubted ancestor of *Sandlingites*, is comparable only if forms like *A.* (?) *teltschenensis* (Hauer) are envisaged. This species is probably quite distinct from the Middle Triassic forms described by J. P. Smith himself, of which *A. drakei* was stated to be " not nearly related to any other species in the American region." This is not surprising, as it is obviously only a malformation.

Hyatt (1900) included the Clydonitinae as a sub-family in Tirolitidae and added to the diagnosis that the costae were interrupted on the venter, which was often channelled. But though this applies to *Clydonites* and *Sandlingites*, it scarcely describes *Eremites* Mojsisovics which was included here by Hyatt. This is now referred to the family Buchitidae (see p. 77) ; but *Ectolcites* Mojsisovics, another genus listed by Hyatt, is included in the family Distichitidae. It shows no resemblance either to the two typical genera or to *Eremites*, the type of which at least shows a trachyceratoid venter.

c. Family CLIONITIDAE Arabu (1932), emend.

This family is here taken in a much narrower circumscription than as put forward by Arabu, who included in it genera like *Arpadites*, *Trachyceras* and *Choristoceras* which have all had families of their own for many years. If they are considered to belong to one family, surely a name like Trachyceratidae, in existence since 1894, would have been chosen by anyone conversant with the rules of nomenclature. The present family Clionitidae thus has very little in common with Arabu's comprehensive assemblage ; and the name is adopted simply because it is required for a group of genera ranging themselves around *Clionites* Mojsisovics (1893), just as this genus itself covers a group of species that show close agreement in essential characters with the genotype: *Clionites angulosus* Mojsisovics (1893).

The typically Carnian genus *Clionites* is very much like *Buchites* of the same beds, except for the ventral furrow. Mojsisovics, indeed, thought *Buchites* to be the root-stock of *Clionites* ; yet the latter is common already in the Lower Carnian, and it is more likely that both are derived from a common Ceratitid root, perhaps among the Danubitidae or the Aplococeratidae. The attempt to trace Clionitidae back to the Permian *Paraceltites*, an ornamented group, seems to me entirely miscarried, when there are so many smooth stocks of the Lower Triassic to choose from. *Clionites* is too much of a Trachyceratid, however, already at its first appearance, to be widely separated from its close relations, *Protrachyceras* and *Anolcites* of the Ladinian, which may also retain the entire saddles of their ceratitic suture-lines.

While the typical *Clionites* have few tubercles, if any, the branching of the ribs, increase of the sigmoidal curvature and narrowing of the umbilicus produce various groups of at least sub-generic importance, while increase in tuberculation culminates in the quadri- or quinquetuberculate Norian forms that may be totally unlike the primitive Lower Carnian fore-runners. One of these early forms is the St. Cassian *Amm. acuto-costatus* Klipstein, the holotype of which is in the Museum (see p. 48), and which has been referred by Mojsisovics to *Trachyceras* and later to *Protrachyceras*. In 1914 Welter recorded it as *Clionites* from the Ladinian of Timor, but Diener (1923) referred the same form to *Clionites catharinae* Mojsisovics, and put it into the Middle Carnian. In the holotype of *C. acuto-costatus* (the figure of which in Klipstein was enlarged about three times) the venter is still angular, as in the early part of *C. angulosus*, before the tubercles are developed. Another of the primitive forms is *Trachyceras armatum* (Münster) Mojsisovics (1882), later (1893), included in *Anolcites* but correctly compared by Kittl (1908) to *Clionites*. This is highly tuberculate in the young and thus may be the ancestor of other Trachyceratoid stocks, as mentioned below. In a Gulf of Ismid (Asia Minor) fauna in the Museum (W. Endriss Collection) there are *Clionites* of the type of *C. dobrogeensis* Kittl, together with *Protrachyceras furcatum* (Münster), *P. rudolphi* Mojsisovics, and " *P.*" *acuto-costatum* (Klipstein), as interpreted by Arthaber (1914) ; and in spite of the ammonitic suture-line of *Protrachyceras*, they are very intimately connected.

In the typical *Clionites* the lateral ribbing is single as in *Danubites* and the ribs may end at the siphonal groove with hardly any thickening, or they may have one or even two rows of tubercles on the periphery. The shells then may become compressed, the ribbing may get more sigmoidal, and spiral striation may be conspicuous. These forms lead from what Smith called "merely technically the type" to the multituberculate Norian forms of the *ares*-group on the one hand, and on the other, *via* the slender *berthae*-group and *C. valentini* Mojsisovics, to the genus *Indoclionites*, mentioned below.

The *ares*-group is here separated as a new genus, **Alloclionites** gen. nov. (genotype: *Clionites ares timorensis* Welter, 1914, p. 133, pl. xxxvi, figs. 6, 9. = *Alloclionites* **timorensis** nom. nov.) because a typical example of this species (No. C. 40684) is totally unlike the true *Clionites*, e.g. *C. catharinae* Mojsisovics (No. C. 40620), also from Timor, and even the more tuberculate *C. regularicostatus* Diener (No. C. 40685). In the Timor forms the quadri- or quinquetuberculate ornamentation degenerates on the body-chamber much more than in the smaller Himalayan equivalents and the ventral groove tends to be obliterated.

Some true *Clionites* have recently been described from Nevada (Johnston, 1941), but the Californian species attributed to *Clionites* by Hyatt & Smith (1905) are much more Trachyceratid in ornamentation. They were thus distributed among four sub-genera as follows: *Shastites* Hyatt & Smith, 1905 (sub-genotype: *Clionites compressus* Hyatt & Smith, 1905); *Stantonites* Hyatt & Smith, 1905 (sub-genotype: *Clionites rugosus* Hyatt & Smith, 1905); *Traskites* Hyatt & Smith, 1905 (sub-genotype: *Clionites robustus* Hyatt & Smith, 1905); and *Neanites* Hyatt & Smith, 1905 (sub-genotype: *Clionites californicus* Hyatt & Smith, 1905). To these has to be added *Californites* Hyatt & Smith, 1905 (genotype: *C. merriami* Hyatt & Smith, 1905) which was kept distinct from *Clionites* and unhesitatingly declared to be a direct descendant of the Lower Triassic genus *Tirolites*. *Californites* was also considered to be of especial importance in the phylogeny of *Clionites*, for all spinose members of that group went through a distinct *Californites*-stage. *Californites*, in fact, was held to be the ancestor of *Clionites*.

The *fairbanksi*-group which had been left in *Clionites* s.s. was later (1927*a*) united with the third of the above sub-genera, and Smith then considered them all (and perhaps the whole genus *Clionites*) to be reversionary and degenerate and derived from *Trachyceras*. In that case they would have no place in the present family and might, perhaps, be included in a separate family, "Californitidae," like the special offshoot Clydonitidae, which has forms with a very similar ventral area. But the very young shells of the Californian "*Clionites*" (well represented in the Collection) are much like the larval *C. armatus* (Münster) and the so-called *Californites*-stage is present at 7 mm. diameter, corresponding with Smith's (1927*a*) much larger pl. lxxxii, fig. 15 (of natural size). These young stages, in my opinion, are caenogenetic, and the two *Clionites* features of the Californian forms, namely, the open coiling and the ceratitic suture-line, are not secondary, but primary characters, as in the somewhat similar *Allo-clionites*. They may thus well be left in the family Clionitidae, and since it is advisable, on the one hand, not to reduce *Californites* to a sub-genus of *Traskites* and, on the other, not to reverse accepted nomenclature by including the others as sub-genera in *Californites*, it is proposed to raise *Traskites*, obviously the principal of these four Californian "*Clionites*," to generic rank and to include in it *Shastites*, *Stantonites* and *Neanites* as sub-genera. The differences among them are slight, and they all have that peculiar, fine multituberculate ornamentation of the periphery which is lacking in the ventrally smooth *Californites*. Though small, this is thus distinct from the other four, but there is no resemblance to any bituberculate European *Clionites*.

Dawsonites, which was also included by Smith as a sub-genus in *Clionites*, is here referred to Trachyceratidae (p. 45). It has entire saddles, like *Anolcites*, but is too involute for a *Clionites*. Its possible identity with *Shastites*, suggested by Smith, does not bear closer investigation. Likewise Frebold's (1930*a*) impression of a Spitsbergen Trachyceratid has only superficial resemblance to the Californian "*Clionites*," as the strong ribs would have left their mark as well as the tubercles.

The genus *Indoclionites* Diener, 1916*e* (genotype: *Clionites gracilis* Diener, 1906) is rather distinct from the normal evolute *Clionites*. The genotype was described as occupying an isolated position within that genus, being more involute than any other species. Like *Protrachyceras* (?) *jonkeri* Pakuckas (1928), which probably belongs to *Indoclionites*, *I. gracilis* has the sigmoidal ribs united in bundles at the umbilical end, and single on the periphery.[1] These forms may be developments of the compressed *berthae*-group of *Clionites*, but there is another, parallel group, apparently descendants

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[1] *Sandlingites tuckeri* Diener (1906*a*) seems to be more closely related to *Indoclionites* than to the typical evolute *Sandlingites*.

of *C. valentini* or *Daphnites tristani* Mojsisovics, in which the ribs become auritoid or double between the prominent umbilical and the ventro-lateral tubercles (as in the Gault *Euhoplites lautus*). A specimen labelled *Clionites* cf. *salteri* Mojsisovics, from the *Halorites* beds of the Bambanagh section (No. C. 28680) seems to belong to this unnamed second group. I thought at one time that it might be a misidentified specimen of *C. stantoni* Diener (1906*a*), but this also has only single ribs. The example (No. C. 4850) figured by Salter (in Salter & Blanford's ' Palaeontology of Niti,' 1865, pl. vii, fig. 6) as *Amm. aon* (Münster) represents the inner whorls of the true *Alloclionites salteri* (Mojsisovics), and this is entirely different.

Steinmannites Mojsisovics, 1893 (genotype : *Amm. hoernesi* Hauer, 1849), also at first a sub-genus of *Arpadites*, is close enough to *Clionites* to be included here. The agreement, especially in the suture-line of the Himalayan species of *Allocionites* and *Steinmannites* is striking. In *S. hoernesi* the crenulate edges of the siphonal channel are well marked, and this feature, accounting for the inclusion of both *Steinmannites* and *Clionites* as sub-genera in *Arpadites*, is much more developed in the former than in the group of *Alloclionites ares*. In any case, *Steinmannites* would be out of place in the family Arpaditidae, with its continuous keels.

The genus *Meginoceras* may be mentioned here because it was introduced as a sub-genus of *Steinmannites*. It was, however, later included by McLearn in the genus *Paratrachyceras s.l.*, and it is referred to under Trachyceratidae (p. 42).

Daphnites, like *Clionites*, was established as a sub-genus of *Arpadites*, but is much nearer to the latter, or even to the similar *Klipsteinia*, so far as the two typical species of *Daphnites* are concerned. But in the case of *D. tristani* the resemblance to *Clionites* is considerable, not to the typical *C. angulosus*, but to the forms above described as intermediate to *Indoclionites*. The remaining species of *Daphnites*, the beautiful but unique, suturally unknown *D. zitteli* Mojsisovics, is again quite different, and might even be an extreme *Anasirenites*.

The peculiar genus *Brouwerites* Diener, 1923 (genotype : *Clionites involutus* Welter, 1914) is based on an inflated involute form which does not seem to have any resemblance to the more evolute species of *Clionites*. But by the transitional *B. intermedius* (Welter) and the still less extreme

Clionites paucinodosus and *C. randolphi* var. *timorensis* Welter, *Brouwerites* is connected with the more orthodox species of *Allociionites*. They all have the longitudinal striation characteristic of the genus. The resemblance of *Brouwerites* to forms of other unrelated groups is thus merely a matter of homoeomorphy.

To include the involute *Brouwerites* in the present family merely because of its Clionitid suture-line, may suggest to some that this single character is being stressed unduly, and that it will make the family as artificial a group as it was in Arabu's original reading. On the other hand, if stress is laid rather on the coiling, *Brouwerites* would be excluded from Clionitidae, but would have to have a family of its own, since the Clionitid suture-line prevents closer comparison, for example, with *Sagenites* or some other externally similar genus. This would merely increase the number of families to an undue extent and, in the present case, there are transitions between the extreme *Brouwerites* and *Alloclionites*.

The genus *Glamocites* Diener, 1917*a* (genotype : *G. katzeri* Diener, 1917*a*) can be included in this family only with doubt. The resemblance to *Thetidites*, e.g. *T. brysonis* Diener is so striking that only the very different development of the suture-line prevents direct connection. Even if ceratitic suture-lines (e.g. in the Acrochordiceratidae) are known to have specialized in the peculiar manner of *Glamocites*, the high external lobe forbids comparison with the very low and simple external lobe of *Thetidites huxleyi* Mojsisovics ; and if it is remembered that this form is of Norian age, whereas *Glamocites* is early Carnian, the similarity in ornamentation loses its significance. The same applies to the equally Norian genus *Heraclites*, whose suture-line, at least, is ammonitic and would require but little modification.

There remain for comparison those Californian Clionitids, cited by Diener, in which the ventral groove may become shallow on the outer whorls (though not necessarily in the manner of the "senile" specimen of *Shastites compactus*, figured by Smith) and in which the suture-line may at least show the same general outline as in *Glamocites* (compare *Stantonites evolutus* Smith, 1927*a*, pl. lxvi, fig. 15). These Californian Clionitids are of Upper Carnian age, and thus presumably later than *Glamocites*, but the more typical forms of *Clionites* from the Lower Carnian are not at all comparable. Since Diener himself confessed that it was impossible to place *Glamocites* either with the Tropitida or the Ceratitida, i.e. the Trachyceratida in the writer's classification, it is hoped that the single example known at present will not long remain the only representative of this puzzling genus.

It ought to be added that inclusion of *Glamocites* in Clionitidae could be justified only on the basis of the open coiling, for the suture-line clearly points to Trachyceratidae which, however, are mostly more involute. It is, indeed, out of place in either, but so it would be in Tropitida or in Ceratitida.

D. Family ARPADITIDAE Hyatt (1900).

It may be remembered that Mojsisovics (1896*a*, 1899) considered *Arpadites* to be a polyphyletic genus, traceable to different Ceratitoid root-stocks; and he held that as soon as these stocks could be established, the genus *Arpadites* would be given up. Of course, a genus cannot just be abandoned, but it may have to be emended in the light of increased knowledge. Only, before the various roots of the original comprehensive *Arpadites* could be discovered—and it seems that we have not arrived at this desirable state even at the present day—Hyatt created a family Arpaditidae, and included in it all the original sub-genera of Mojsisovics, except *Clionites*, which appears to have been missed by accident, for it is not referred to any other family. In addition, however, Hyatt referred to this family certain groups now included in Heraclitidae and Cyrtopleuritidae, discussed below, as well as the genus *Bosnites*, which is now (p. 8) assigned to the Noritidae. This last genus obviously puzzled Hyatt, who included it only with doubt, apparently because it did not show any "tendency to form a channelled venter, bordered by two ridges which may be either tuberculose or smooth." This was a very good definition of a purely morphological family Arpaditidae.

Hyatt & Smith, soon after (1905), abandoned the family without a word of explanation, treating *Arpadites* merely as a genus of the family Ceratitidae. Smith, in 1913, reduced Hyatt's family to a sub-family within the Ceratitidae, but listed the same 12 genera with the exception of *Bosnites* (which was then attached to the Carnitinae of his Pinacoceratidae). In 1927*a* Smith once more considered *Arpadites* to be merely a genus in the Ceratitidae.

Now, with regard to the polyphyletic elements in the original family Arpaditidae, the early Ladinian-Carnian genera like *Arpadites* itself and *Klipsteinia* seem to form one group characterized by more or less ceratitic suture-lines and ventral keels that may be entire or crenulated or mere edges of the siphonal groove simulating keels. Then there are the genera that look like these early Arpaditids, e.g. *Daphnites* and *Drepanites*, but are of much later date and have certain peculiarities, not found in their fore-runners, so that they are probably not so very closely related. Finally there are genera like *Dittmarites* and *Trachypleuraspidites* that have continuous keels and thus satisfy a morphological definition of Arpaditidae, but by their other characters are apparently closer to the persisting Trachyceratidae than to the earlier *Arpadites* itself. This is stating the case far too simply, for there are the complications of the suture-line which may be fully developed or reduced, ceratitic or ammonitic. It is sufficient to examine the two species of *Arpadites* from the Himalayas, described by Mojsisovics (1896*a*) as *A. lissarensis* and *A. stracheyi*, to see that there is great variation within *Arpadites* itself. The grouping here suggested is thus probably capable of considerable revision when more information is available. Some of the genera (e.g. *Dittmarites*) are represented in the Collection by only a few specimens, too precious to be broken up for study; *Münsterites* is one of the few genera of which there is not a single example; and in many cases duplicates are not abundant enough for section-cutting.

The typical genus is *Arpadites* Mojsisovics, 1879*a* (genotype: *Amm. arpadis* Mojsisovics, 1870), comprising flat discoidal shells with feeble radial or faintly sigmoidal ribbing and a shallow siphonal furrow between two keels. This typical *arpadis*-group, including the very evolute *A. lissarensis* Mojsisovics, may be made to comprise the forms described by the same author as *A.* sp. ind. ex aff. *A. szaboi* (1882, pl. xxv, figs. 16, 28)[1] and *A. szaboi* itself, as well as the *cinensis*-group, in which the ventral keels are far from sharply developed, according to the Esino Kalk examples in the Collection. But the young of this typical Ladinian group are essentially the same, except that the ventral groove appears before the whorls are compressed.

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[1] *A.* ex aff. *A. arpadis* on the plate.

A fore-runner of the typical *arpadis*-group is the early *Arpadites liepoldti* Mojsisovics (1882, pl. viii, fig. 1 ; pl. ix, fig. 9) from the Ladinian zone of *Trachyceras reitzi*. Since this form obviously cannot be attached to one of the Carnian groups of *Arpadites*, recognized by Mojsisovics in 1893, a new name : **Hyparpadites**, gen. nov. (genotype : *Arpadites liepoldti* Mojsisovics, 1882, p.53, pl. viii, fig.1, pl. ix, fig. 9) is here suggested. Diener considered *A. liepoldti* to be a true *Ceratites*, because it had three lateral lobes instead of two, as in the true *Arpadites*, and because the keels were not real keels ; but they are at least as continuous as in the Esino Kalk specimens of the *cinensis*-group.

The genus *Edmundites* Diener, 1916*c* (genotype : *Arpadites rimkinensis* Mojsisovics, 1896*a*) is here adopted for the Indian form with ammonitic suture-line and sigmoidal folds. It probably connects with *Arpadites* through *A. stracheyi* Mojsisovics (1896*a*), which has a ceratitic suture-line and therefore cannot be a variety of the same species as *E. rimkinensis*, as Diener thought. The holotype of *A. stracheyi*, refigured by Mojsisovics from a plaster-cast, is in the Collection, together with the other two examples figured by Salter (in Salter & Blanford, 1865), and seven additional specimens and fragments. I agree with Diener that the comparative smoothness and the occasional elliptical shape are not of specific importance, but the suture-line is not brachyphyllic, as in *Edmundites*.

In the holotype of *A. stracheyi* the last suture-line is exposed just over three-quarters of a whorl away from the end (at 27 mm. diameter), and it is essentially like the suture-line of *A. cinensis* Mojsisovics. In Salter's drawing (fig. 3*g*) the saddles are not slender enough, but the suture-line of the smaller example (fig. 3*d*, wrongly connected up with fig. 3*a*) is tolerably accurate, though the umbilical saddle seems to have been added by the artist from one of the larger fragments. This young example (fig. 3*e*), on account of the lack of constrictions, has no resemblance to *Asklepioceras*.

The genus *Klipsteinia* differs from the typical *Arpadites* because the characteristic feature, i.e. the acquisition of crenulated keels on the venter, is unusually delayed. As Mojsisovics pointed out, the young of *Klipsteinia* may therefore easily be confused with immature "*Dinarites*" of the same beds at the base of the Carnian, e.g. "*D.*" *eduardi* Mojsisovics. But I can see no affinity between the Mediterranean *Klipsteinia* and the earlier, Arctic group of spiniplicate Dinaritids, i.e. the genus *Olenikites*, with which Mojsisovics connected it in 1886. *Klipsteinia* is not even considered to be related to *Aplococeras* (group of "*Dinarites*" *avisianus* Mojsisovics), with which some authors have included "*D.*" *eduardi*. Though this is much nearer in date of existence, its ornamentation does resemble that of *Olenikites*, if only superficially. As mentioned above (p. 37), however, the Ladinian-Carnian "Dinaritids" attach themselves more or less naturally to some Anisian Ceratitid derivative (*Pseudaplococeras* and *Metadinarites*) and are kept apart from the Trachyceratida.

The genus *Klipsteinia* Mojsisovics, 1882 (genotype: *K. achelous* Münster sp., 1834) includes a group of forms of the *aon* zone of St. Cassian; and it is well represented in the Klipstein Collection, though not by such large and well preserved examples as were figured by Mojsisovics. The group does indeed seem "narrowly defined," if interpreted by the example figured in Mojsisovics's pl. xxv, fig. 25. It shows that the genotype species has not only the crenulate keels found in so many of these Arpaditids, but acquires tubercles at the ventro-lateral shoulders. This feature, however, is not found in *K. nataliae* which comes closest to the true *Arpadites*, whilst *K. karreri*, *K. hirschi* Mojsisovics, and *K. boëtus* (Münster) may well be compared to the numerous young examples of *Trachyceras* and *Protrachyceras* found in the same beds. For instance, the six specimens of "*C. boetus*" in the Klipstein Collection (labelled, by Klipstein, *Ammonites karsteni*) are possibly all different, but five of them show a general resemblance to Münster's type, refigured by Mojsisovics. The figured example, however, to which the name *karsteni* should be restricted, has two very regular, strong rows of clavate tubercles on the venter, parallel, and separated from the ribs. The seven specimens of *Ceratites busiris* Münster (identified by Klipstein), again show differences among themselves, but are more involute young Trachycerata of the same type. On the other hand, three examples, labelled by Klipstein *Ceratites okeani* Münster (one of 21 mm. diameter), represent what I would consider typical *Klipsteinia*, with goniatitic or only slightly sub-divided suture-line, i.e. *Arpadites*, as generally understood, but with crenulate, not entire keels. At diameters of less than 15 or 20 mm. the differences from young *Protrachyceras basileus* (Münster) and *Ammonites bidenticulatus* Klipstein (in the Collection) are small, but the external saddle in these becomes sub-ammonitic already at about 7 mm. diameter.

Another "*Arpadites*" without true ventral keels at all stages, and not even the crenulate keels of *Klipsteinia*, but merely a ventral groove, is *Trachystenoceras* Johnston, 1941 (genotype : *Arpadites gabbi* Hyatt & Smith, 1905). The periphery, however, appears crenulate in side-view, except in large examples (of over 50 mm. diameter), and the groove then becomes shallow. A small Nevada example in the Collection shows fine sigmoidal lines of growth between the peripheral crenulations and the umbilical bulges, which suggests bundling of the ribbing, now completely lost, at the inner end, as in *Daphnites*. The umbilicus is small.

Silenticeras McLearn, 1930 (genotype : *S. hatae* McLearn, 1930), first introduced as a sub-genus of *Daphnites* Mojsisovics, differs from the more involute *Trachystenoceras* in having a deep, ventral groove. Two examples in the Collection, from the *Nathorstites* Beds of the Peace River district, show a radial line like *Daphnites*, being less sigmoidal than that of *Trachystenoceras* but with extreme peripheral projection. The ventral keels are almost entirely smooth, as is the umbilical edge. The body-chamber occupied three-quarters of the last whorl ; the ceratitic suture-line is short like that of *Daphnites*, with one wide lateral lobe. The umbilicus is 26 per cent. of the diameter.

While the six genera, above discussed, are a fairly homogeneous group and might be considered a sub-family within the Arpaditidae, the following four genera are more doubtful, and differ too widely among themselves to be grouped together in another sub-family. There is, first of all, the genus *Dittmarites* Mojsisovics, 1893 (genotype : *Ceratites rimosus* Münster, 1841) which has, probably wrongly, been taken to include those spectacular, large Carnian-Norian forms, of which the Museum possesses examples in *D. trailli* and *D. trailliformis* Diener, from the Tropites Limestone of Byans. These simulate the falcoid ribbing of *Paratrachyceras*, and their only claim to inclusion in Arpaditidae is the presence of continuous ventral keels, since even the suture-line is ammonitic, as in the Trachyceratidae. But even the early genotype, the Lower Carnian *Dittmarites rimosus*, as figured by Mojsisovics, is probably not a descendant of the true *Arpadites*. The young *A. rüppelii* (Klipstein) assigned to

Dittmarites by Johnston, has not even keels, but only a furrow, according to the originals in the Klipstein Collection and Mojsisovics's figures, which are quite correct.[1]

A genus described as most nearly allied to the group of *Arpadites rimosus*, i.e. to *Dittmarites*, is *Trachypleuraspidites* Diener, 1906*a* (genotype: *T. griffithi* Diener, 1906*a*), also cited erroneously as "*Pleuraspidites.*" The two genera, *Dittmarites* and *Trachypleuraspidites*, although apparently very distinct, are really connected by many features; but whereas the former has no tubercles at all, the latter, at larger diameters, develops the multituberculate ornamentation of *Trachyceras*. The continuous keels, bordering a very inconspicuous siphonal furrow, then form a minor feature of the shell, and the suture-line also is clearly Trachyceratid. The reason for excluding *Trachypleuraspidites* from the family Trachyceratidae, then, is that it is connected with *Dittmarites* which has no tuberculation at all, and that until it attains a considerable size, the ventral furrow is deep and wide, while, then, there are only one or two tubercles on the ribs. These, however, are lateral, not peripheral.

Another group of Arpaditids, the "*circumscissi*," have been separated from the *rimosus*-group as *Asklepioceras* Renz, 1910 (genotype: *Arpadites segmentatus* Mojsisovics, 1893). As usual, the ventral furrow, not accompanied by definite keels, is the principal feature, but the Carnian species of *Asklepioceras* (which begins in the Ladinian) become involute, often sub-globose, and with their characteristic constrictions look very different from their presumed discoidal ancestors. Turkish examples of *A. segmentatum*, *A. circumscissum* (Mojsisovics) and *A. squammatum* Arthaber, support the contention that while *Asklepioceras* is quite distinct from *Dittmarites*, it cannot be included as a sub-genus in *Arpadites*. The smooth unconstricted *Klipsteinia* Mojsisovics is scarcely comparable to *Asklepioceras*, morphologically, but it has a similar suture-line with a high and wide second lobe, according to examples in the Klipstein Collection.

The single species constituting the genus *Münsterites*[2] Mojsisovics, 1893 (genotype: *Arpadites ectodus* Mojsisovics,

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[1] *Amm. rüppelii* is figured in Klipstein's pl. ix, fig. 2, and the erroneous naming of this as *Amm. noduloso-costatus* and of fig. 3 as *rüppelii* misled, for example, Pictet (1854) who thought that it scarcely differed from *Amm. aon.*

[2] *Muensterites* in Diener's Catalogue (1915*a*, p. 207). This is wrong, according to Art. 20.

1893) may be merely an extreme of the *interscissi*-group, with loss of the bicarinate venter. As in the case of the young "*A.*" *rüppelii* (Klipstein), above referred to and included in *Dittmarites*, the genus *Münsterites* may be provisionally left in Arpaditidae.

What has been said concerning the four genera just discussed applies to the classification of the next group of genera, left in Arpaditidae because *Drepanites* and *Dionites*, at least, have been declared by Mojsisovics to be derived from the group of *Arpadites* "*rimosi.*" There is a faint resemblance to that group, that is to *Dittmarites*, in the involute, discoidal aspect and the sigmoidal, if feebler ribbing of *Daphnites* and *Drepanites*. Diener (1920*a*) figured a *Drepanites* (?) nov. sp. ind., an interesting form which was considered transitional to *Daphnites* as well as to *Dionites* ; it has a deeply excavated ventral furrow and an inflated whorl-section at a diameter too large for an immature *Drepanites* (being a body-chamber fragment). To my mind it shows not only the close connection between these Norian types, especially *Dionites*, and their Trachyceratid ancestors, but demonstrates that in the present state of our knowledge, a workable classification must have some elasticity. In the circumstances it would be premature to separate the next four genera into another distinct subfamily, especially as *Drepanites*, the only genus that is fairly well represented in the material before me, has its special peculiarities that remove it widely from the spirally tuberculate *Dionites*.

The most striking feature of the genus *Drepanites* Mojsisovics, 1893 (genotype : *D. hyatti* Mojsisovics, 1893) is an unaccountable resemblance to its equally discoidal contemporaries *Hauerites* and *Cyrtopleurites* which are not directly related, but have similar, finely punctate, peripheral edges and crescentic, *Oppelia*-like ribbing. It is true that the venter itself is different in the forms less specialized than the very typical *D. bipunctulus* (Quenstedt) which is represented in the Collection by some fine examples. But the smaller, fatter, and less attractive forms like *D. aster* (Hauer) soon bring us back to the Arpaditidae. The suture-line is ammonitic, sometimes with a suggestion of an adventitious saddle, and essentially that of *Trachyceras*. A species like *D. saturnini* Diener shows that the tabulate venter may finally become rounded.

A median section of a young example of *D. hyatti* Mojsisovics (No. C. 5707*b*) is very similar to corresponding sections of *Trachyceras* and *Sirenites* in its rapid rate of growth and high, biconvex septa. The moderately thick siphuncle is nearly central in the second whorl, as in *Sirenites agriodus* (v. Dittmar) as figured by Schindewolf (1931), but quickly becomes subventran in the third whorl, while it is not quite ventral even at the end of the septate stage, at about 25 mm. diameter. There are, then, 20 septa, irregularly spaced, but on the whole gradually approximating ; the whorl before (third whorl) has only 13 septa. The protoconch is rather small (about ·4 mm. diameter).

The equally Norian genus *Daphnites* Mojsisovics, 1893 (genotype : *D. berchtae* Mojsisovics, 1893) is rather distinct from the last genus and includes only a small number of species. Even among these, however, the typical species does not so clearly show the keel-like edges of the ventral furrow as some of its varieties or the more representative *D. ungeri* Mojsisovics. The more coarsely ribbed *D. tristani*, again, is transitional to forms included in *Clionites*, whereas the totally aberrant *D. zitteli*, apart from its deep ventral furrow, has no resemblance to any Arpaditid. Unfortunately, there are only poorly preserved Sicilian examples of *Arpadites* (*Daphnites*) *kittli* and *A.* (*D.*) *toulai* Gemmellaro, before me and it is not easy to compare these dwarf-species (perhaps Clydonitids) with the larger forms above described. From the systematic point of view it does not make any difference whether the falcoid ribs unite in bundles on the umbilical edge, as in the typical species, or remain single or bifurcating, with an occasional intercalated rib as in *D. flaviani* Diener. There is no tendency to lose the ribbing on the side, as in other Arpaditids.

The genus *Dionites* Mojsisovics, 1893 (genotype : *Arpadites caesar* Mojsisovics, 1893) was also originally introduced as a subgenus of *Arpadites*, like the equally involute *Drepanites* and *Daphnites*, but it is much less like the typical Arpaditids. *Dionites*, which has an ammonitic suture-line, with the usual wide lateral lobe as the most conspicuous element, includes a highly specialized group of spirally ornamented ammonites. There is no resemblance to the group of *Arpadites rimosus* = *Dittmarites*, from which it is said to be derived. The ventral tubercles or clavi may unite into crenulated keels, as in Clionitids (*Steinmannites*), but they do not form continuous keels as in the true Arpaditidae. Moreover, there is the linear arrangement of the tubercles, as in *Trachyceras*.

There is distant resemblance to the form figured by Hyatt & Smith as *Sirenites lawsoni*, with longer second lateral lobe and slenderer saddles than the younger (Norian) genus *Dionites*. This Californian species also has bullae at the ventral groove, instead of clavi; but the general Trachyceratid appearance of the magnificent large example of *D. caesar*, figured by Mojsisovics, suggests inclusion of the genus in Trachyceratidae as much as in Arpaditidae.

Finally, there is the genus *Xenodrepanites* Diener, 1916*a* (genotype: *Drepanites schucherti* Diener, 1906*a*) which was described as constituting a distinct group within *Drepanites*, but was not separated sub-generically till ten years later. It is here raised to generic rank, as it differs very considerably from *Drepanites*. It is rather peculiar that Diener should also compare *X. schucherti* to *Hauerites*, when it is externally and internally so different and even lacks the characteristic punctate ventral edges of *Drepanites*, whilst *X. schucherti* and its companion species, *X. eastmani* Diener, with more continuous costation, have a comparatively open umbilicus. With their flat, discoidal shape and crenulate peripheral keels they are more like typical Arpaditidae than e.g. *Dionites*. The suture-line is distinct, but not against inclusion in this family. The saddles are almost ammonitic, but retain the ceratitic outline, the incisions are deep in the lower half, but the tops of the saddles are only very finely serrated.

E. Family LECANITIDAE Hyatt (1900).

The genus *Lecanites* Mojsisovics, 1882 (genotype: *L. glaucus* Münster, 1834), plain in every way, with a goniatitic suture-line, has perhaps had more widely different interpretations than any other group of ammonites. Already, in 1884, Zittel doubted the original inclusion in Lytoceratidae; and Waagen (1895) stated that the suture-line did not furnish "the slightest indication for supposing an affinity in that direction." Waagen, however, thought the Lower Trias of the Salt Range corresponded probably with the European Upper Triassic beds in which the single species of *Lecanites* had been found, a supposition that would have strained credulity even in the case of a much more distinctive genus of ammonites. Only two years later, Diener (1897*a*) stated that Waagen had " demonstrated " the close relationship of (his) "*Lecanites*" to the Meekoceratidae in so convincing a manner that he followed his lead in placing that genus in the sub-family Meekoceratinae. Hyatt & Smith (1905) and J. P. Smith (1914) also included *Lecanites* in the Meekoceratidae, later (1932), in Xenodiscidae ; but the statement that *Lecanites*, even at maturity, had a strong resemblance to *Gephyroceras*, was about as helpful as saying that it was an ammonoid and not anything else. The Lower Triassic groups previously referred to *Lecanites* have already been dealt with in Part IV. Smith, in 1914, described only Middle Triassic species and these also have been discussed above (see p. 37). As has been mentioned, it is believed here that the Anisian forms of " *Lecanites* " are no more related to the true Carnian *L. glaucus* than is *Aplococeras* or any other so-called *Dinarites* of Middle or Upper Triassic age.

Among ten specimens of *L. glaucus* in the Klipstein Collection, seven uncrushed examples and fragments, and one crushed example, may be accepted as belonging to the species in Mojsisovics's interpretation, taking his fig. 4 (pl. xxx), and Laube's (1869, pl. xxxvii, fig. 9) enlarged figure as representative. The latter well shows the extremely fine lines of growth which, of course, are rarely preserved, so that the average specimens are entirely smooth. *L. tenuissimus* (Klipstein) differs merely in its wider umbilicus (48 per cent. of the diameter instead of 42 per cent.). There is no specimen exactly like Klipstein's figure among his ten examples and only one, of 9·5 mm. diameter, that shows the wide umbilicus, the others being *L. glaucus* or else too small to be identified with either. On the other hand, Mojsisovics's fig. 5 (pl. xxx) represents the form called *Goniatites* ? *iris* by Klipstein. There are three fragments in the Collection and the only one that could be the figured example, representing a shell of 15 mm. diameter, is certainly not identical with *L. glaucus*, as Laube and Mojsisovics held. The very delicate striation is well preserved on the iridescent test, and is approximately as shown in Klipstein's not very successful figure. But the conspicuous feature about *L. iris* is the presence of a distinct ventro-lateral edge. The strongly falcoid striae of the parallel sides change direction on this edge and are continued across the arched periphery with a slight sinus directed forwards, being stronger than on the side except just at the edge. This is accompanied by a spiral depression which in a second example appears just as drawn in Mojsisovics's fig. 5.

Two of Klipstein's examples of *L. glaucus* have crenulate venters like many so-called *Arpadites*, and they belong to two different species. While still smooth on the sides at about 18 mm. diameter, one has part of the body-chamber and shows denticulated first lateral lobes, on the septate part, inside the line of involution, so that the umbilicus was only about 33 per cent. of the diameter. They are probably immature *Klipsteinia*, but cannot be matched by other named specimens in the Collection. Their reference to *Lecanites glaucus* is obviously due to some error.

Goniatites bronnii Klipstein (1843, p. 141, pl. viii, figs. 18*a–c*) was included in the synonymy of *Ammonites eryx* Münster by Laube and Mojsisovics, but, as was pointed out in the original description, it is characterized by an exceedingly fine striation. This is greatly exaggerated in the illustration, as are the very faint, periodic constrictions, but the ventral area is flattened, as in *Lecanites iris*, not narrowly rounded as in *L. glaucus*. As there is no difference in the suture-line, this form also must be included in the genus *Lecanites* and not in *Badiotites*, like *Ammonites eryx*. The umbilicus is reduced to only 25 per cent. of the diameter in the only one of Klipstein's four examples which can be the original of his figure ; a larger one, of 16·5 mm. diameter, has suffered from corrosion. *Goniatites radiatus* Klipstein (1843, p. 140, pl. viii, figs. 15*a–c*) is still more involute and almost completely smooth, but it has pronounced constrictions and an undoubted median saddle in the external lobe. The form is certainly less inflated than Mojsisovics's two specimens identified with *G. radiatus* (pl. xxviii, figs 12–13), and there is no indication of serration of the principal lobe. In any case the suture-line has no resemblance to that of the true *Dinarites*, but in view of the small size of the examples available, I agree with Mojsisovics that it is not impossible that they represent the inner whorls of some form of *Klipsteinia*.

Goniatites dufrenoii Klipstein (1843, p. 142, pl. viii, figs. 20*a–c*), also included in the synonymy of *Ammonites eryx* by Laube and Mojsisovics, has not been recognized in the Collection. At least, among the eight specimens thus labelled by Klipstein, none agrees with the figure or description, and, in any case, the short lateral lobe of the rather distinctive suture-line is not that of a *Lecanites* or of *Ammonites eryx*. The largest of the eight specimens mentioned is very evolute and has half a whorl of body-chamber at 7 mm. diameter. It could belong to *Lecanites tenuissimus* or *Goniatites wissmanni* Klipstein (*non* Münster)[1] and has only one lobe on the side, the umbilical suture following almost immediately on the lateral saddle, whereas in *Ammonites eryx* three saddles are visible in side-view. Two of the examples are young *G. beaumontii* and the remaining five are too immature to be definitely referred to any one species rather than another.

Lecanites trauthi Johnston (1941) seems to be a transition between *L. glaucus* and *Badiotites*, at least morphologically; for its suture-line has both lower saddles and shallower lobes, while having the same goniatitic outline. From the description and the figures it appears that the faintly sigmoidal ribs are broadening towards the venter which they do not seem to cross. The venter is stated to be somewhat sharpened, though not acute. Comparing *L. trauthi* with the figure of *Ammonites eryx* in Quenstedt (1849, pl. xviii, fig. 2), we note that the ribs of the former do not actually run up to the smooth siphonal band which takes the place of a keel in *Ammonites eryx*. Also it may be noted that the original of Johnston's fig. 17 has comparatively coarse ribs on the inner whorls, whereas the two examples of figs. 18 and 20 (both of which have been stated to be the type on pp. 451 and 455) have more finely ribbed or smooth early volutions.

Before discussing the variations observed in the group of *Ammonites eryx*, it may be mentioned that the genus *Badiotites* Mojsisovics, 1882 (genotype: *Ammonites eryx* Münster 1834) was referred by Hyatt (1900) to a separate family Badiotitidae, but the inclusion in the same family of the genus *Doricranites* Hyatt (see Part IV, p. 382) seems rather curious, as this is neither discoidal nor involute. The development of the suture-line, as later shown by Schindewolf (1929), is slightly different in the two genera *Badiotites* and *Lecanites*, though the adult suture-line is almost identical. The numerous examples in the Collection show that there is, of course, no "keeled venter," as stated in the family diagnosis in Hyatt, and as shown in the misleading drawings of Zittel's text-books from 1884 onwards. The appearance of the

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[1] The true *Goniatites wissmanni* Münster, as figured by Mojsisovics, is probably an immature *Klipsteinia*. Only Klipstein's largest example resembles *L. tenuissimus*; the other two are too small to be definitely identified, but one may be a young *L. glaucus*.

periphery, in fact, is best illustrated in Quenstedt's figure, already cited, for some of Laube's and Mojsisovics's examples show the peripheral costation almost continuous across.

Curiously enough the only specimen labelled *Goniatites erix* M. (*sic*) in the Klipstein Collection does not belong to this group at all. It is a fragment of probably "*Dinarites*" *edouardi* Mojsisovics,[1] but (at 18 mm. diameter) has both the lobes (of the side) denticulated. On the other hand, there are at least four unnamed examples of *Badiotites eryx* in the Klipstein Collection, part of a set of ninety fragments of "ammonites and goniatites" which were marked: "still to be compared; could easily yield another six to eight species." Klipstein, thus, could not have interpreted Münster's species correctly, yet he described *Goniatites beaumontii* Münster as being very similar to "*G. erix.*" They have been considered synonyms by Laube and Mojsisovics, and eight of the nine specimens of *G. beaumontii* in the Klipstein Collection would be included by most authors in *Badiotites eryx*. The ninth, showing the complete suture-line, figured by Klipstein (fig. 8*c*), is slightly coarser and belongs to that variety (labelled *Goniatites furcatus* Münster, by Klipstein) in which stronger ribbing is combined with ventral, linguiform, processes rather than a continuous ventral ridge. This last form, Klipstein's *Goniatites* ? *infrafurcatus*, is represented by the figured example (pl. viii, fig. 9) and two other specimens which again cannot be separated from *B. eryx*.[2] The same species includes nine of the ten examples of *Goniatites suprafurcatus*, but the figured example (pl. viii, fig. 10) is distinct. It was labelled (by Crick) *Trachyceras armatum* (later altered to *Anolcites armatus*), evidently accepting Mojsisovics's identification, but there is no real resemblance.

All this confirms that *Lecanites* and *Badiotites* are not separable into two distinct families. But the probable rootstock, persisting through Carnian time and including, possibly, "*Dinarites*" *radiatus*, is as yet very incompletely known.

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[1] Of three examples of this species obtained from the Naturhistorisches Museum in Vienna (also from the Stoures Beds) only one is comparable, the other two being more inflated, like Mojsisovics's smaller examples of *Klipsteinia achelous* (Münster). As it happens, the same could be said of the three examples of "*Ceratites*" *achelous* in the Klipstein Collection, two of which are more inflated than the third. The difference between that species and "*Dinarites*" *eduardi*, then, in the young stage, is one of thickness only.

[2] Klipstein's *Amm. cingulatus* (pl. vii, fig. 6) is in the Collection, and is another worn *B. eryx*.

It may have given rise to *Klipsteinia* on the one hand, and to Lecanitids on the other, in addition to groups included in Buchitidae and other Trachyceratida. But *Lecanites* is quite unconnected with the American forms attributed to that genus by J. P. Smith (see *Pseudaplococeras*, p. 37), and almost equally certainly has nothing to do with "*L.*" *sibyllinus* and *L. loczyi* Frech (1903*a*). The latter was considered by Diener to be indeterminable, so Frech's facile comparison with *Lecanites* and *Ophiceras*, both quite different, fails to impress. The former species was probably also entirely misinterpreted, but the description is inadequate.

It is difficult to see why J. P. Smith (1927*a*) should have called *Badiotites* one of the least known genera in all the Upper Triassic fauna. But I agree with him in considering Whiteaves's assignment of *B.* ? *carlottensis* (apparently a crushed Haloritid) to the genus *Badiotites* " most improbable."

There is no duplicate specimen of *Lecanites glaucus* available for sectioning, but a slide of *Badiotites eryx* was prepared and showed a thin siphuncle which had not quite reached the venter at 2·5 mm. diameter, much as in a section of *Sirenites* aff. *agriodus* (Dittmar). The increase in whorl-height is rapid and there are only 10 septa at 12 mm. diameter, the first six (on the earlier half) arranged in three conspicuous pairs. These are followed by six more pairs on the next inner whorl, separated by wide gaps ; but soon after the preservation changes from pyrites to brown, opaque calcite, so that the innermost whorls (diameter = 1·25 mm.) are obscured. The test is abnormally thick even then, and there is no sign of any constrictions, so numerous in the young *Klipsteinia*.

F. Family HERACLITIDAE Diener (1920*b*).

This family was first established as a division *Heraclitea* within the sub-family Dinaritinae of the family Ceratitidae, including, besides *Heraclites* itself, the genus *Cyrtopleurites*, with the sub-genera *Hauerites* and *Acanthinites* and, by implication, *Tibetites*. Hyatt (1900) referred *Heraclites*, *Cyrtopleurites* and *Acanthinites* to a family Arpaditidae, together with part of Mojsisovics's division *Dinaritea* (of the sub-family Dinaritinae), but he separated *Tibetites* in a distinct family, Tibetitidae, with *Anatibetites*, *Paratibetites* and *Hauerites* as distinct genera.

The family name Heraclitidae was used by Diener (1920*b*, 1923) and Pakuckas (1928), and was not only attributed to Mojsisovics, but it was made to include the Tibetitids, in addition to *Heraclites* and *Cyrtopleurites*. The introduction, by Diener, in 1925, of the family Cyrtopleuritidae, again ascribed to Mojsisovics, thus only aggravated the nomenclatorial tangle. For since Diener did not even mention the genus *Heraclites*, it is impossible to know whether he had meant to separate it from the Cyrtopleuritidae, the family diagnosis being decidedly against inclusion of *Heraclites*. This makes it necessary to justify the present use of the family name.

Heraclites is evolute, a normal "Ceratite" in the older interpretation, with half a whorl of body-chamber and a flattened periphery, after the earlier stages with bicrenate venter. Even after the loss of the two rows of clavi, bordering the ventral furrow the ventro-lateral rows remain for a time, and the siphonal groove may persist, though faint, and it is bridged by the costae across the periphery. At diameters of between 90 and 210 mm. the ventral area is smooth and flattened. *Heraclites* has brachyphyllic or dolichophyllic suture-lines, and, as Diener (1906*a*) has pointed out, the group of *H. robustus* shows saddles provided with deep digitations, imparting to them a very characteristic shape, such as is seen in scarcely any other Triassic ammonite. In the group of the "*suavicostati*," the saddles seem to be less deeply serrated, but the suture-line of only one species (*H. poeschli* Hauer sp.) has been figured ; it is not strikingly different from that of the forms of the *robustus* group, and there is no suggestion of splitting-up of the external saddle, but the second lateral saddle is very short in all of them.

In order to understand Mojsisovics's interpretation of his genus *Heraclites*, it ought to be recalled that in 1879(*a*) he included in it not only *H. robustus* and *H. poeschli* (Hauer) but *Ammonites foliaceus* Dittmar, and *Clydonites quadrangulus* Hauer. The same four species were listed by Zittel (1884), with an unnamed fifth. It would be interesting to know this fifth species, for it might explain the statement that the saddles of *Heraclites* were entire. Mojsisovics, in 1893, widely separated the last two species named, putting *Ammonites foliaceus* in a new genus, *Metatirolites*, and leaving *Clydonites quadrangulus* in the genus *Ceratites* (*Dinarites*), which made them members of two different sub-orders, Dinaritida and

Tirolitida. Yet the closely similar *Ceratites subpygmaeus* Mojsisovics, which he believed to be possibly a *Heraclites*, and which Diener (1915*a*) listed as *Epiceratites* (see p. 77), was, like *Clydonites quadrangulus*, referred to *Metatirolites* by both J. P. Smith (1927*a*) and Pakuckas (1932). Clearly, the former author's dictum that *Metatirolites* undoubtedly descended from *Tirolites* is about as helpful as his placing of *Metatirolites* between *Arpadites* and *"Polycyclus."*

There is, thus, the typical genus *Heraclites* Mojsisovics, 1879 (genotype: *Ammonites robustus* Hauer, 1855*a*), more or less isolated, for the sub-genus *Gümbelites*, established by Mojsisovics in 1896, belongs to quite a different family, as below mentioned (p. 108). Now Mojsisovics, himself, described *Heraclites* as a descendant of *Ceratites* and thought that the Arctic-Pacific group of the *Ceratites geminati* (= *Gymnotoceras*) must be considered to be the genetically most nearly related group. At the same time, Mojsisovics thought it probable that *Cyrtopleurites* and *Heraclites* were descended from common ancestors and became differentiated independently in different directions.

While this relationship may be accepted, the writer is not at all convinced that the trachyceratoid appearance of, e.g. *Heraclites bellonii* Mojsisovics or of *H. sundaicus* Diener, does not reflect real affinity with the Trachyceratida, just as the resemblance between *Cyrtopleurites* and *Sirenites* is not merely a case of homoeomorphy, as Mojsisovics thought. All the same, as the separate family name Cyrtopleuritidae now exists, it is here adopted, but, of course, it can not include Tibetitidae, which family name dates from 1900.

G. Family CYRTOPLEURITIDAE Diener (1925).

This name, attributed to Mojsisovics apparently by error, was first used by Diener, who not only included in it the genus *Cyrtopleurites* Mojsisovics, 1892 (genotype: *C. bicrenatus* Hauer sp., 1855*a*), but the various Tibetitids which fall within Hyatt's family Tibetitidae, dating from 1900. No doubt, Diener would have accepted this family, had he remembered its existence, but as already mentioned, his inclusion, only two years earlier (1923), of all these genera in a family Heraclitidae, also wrongly attributed to Mojsisovics, has not, to the writer's knowledge, been disavowed. Also included here is the genus *Acanthinites* Mojsisovics, 1893 (genotype: *A. excelsus* Mojsisovics, 1893) which was still cited as a sub-genus of *Cyrtopleurites,* in Mojsisovics's original interpretation, by Diener in 1920(*b*), although Hyatt had adopted it as a distinct genus already in 1900.

In 1923 Diener also described *Acanthinites* as a separate genus, but he then included in it, as a sub-genus, *Himavatites* Diener, 1906*a* (genotype: *H. watsoni* Diener, 1906). The peripheral aspect of the Timor *H. welteri* Diener, described at the same time (1923), makes it advisable to regard *Himavatites* also as a distinct genus.

The three genera named have ammonitic suture-lines with the characteristic large lateral lobe of the Trachyceratida in general. It seems best to keep them separate from both the Heraclitidae and the Tibetitidae.

The Collection includes examples of *Cyrtopleurites bicrenatus* (Hauer) from the Mojsisovics Collection (Nos. C. 5729*a–c*), and of *C. freshfieldi* Diener from the *Tropites* Limestone of Byans (Nos. C. 28666–7).

When Mojsisovics (1893) first proposed the name *Hauerites*[1] it was for the group of *Cyrtopleurites rarestriatus* (Hauer, 1850) which thus became the type of the sub-genus. Hyatt (1900) raised *Hauerites* to generic rank and significantly placed it in the family Tibetitidae, but its subsequent vicissitudes, first in Hyatt & Smith (1905) and then in J. P. Smith (1927*a*, 1932), reveal a complete misunderstanding of *Hauerites.* It culminated in Smith's creation of a family Haueritidae, including even Lower Triassic and other unrelated elements, calling it a substitute for the family Carnitidae, which he rejected although it dates from 1911, and stating that the family Haueritidae was not allied to *Cyrtopleurites.* Arabu (1932) adopted Smith's family, tentatively, and apparently, as a leiostracous (Pinacoceratoid) stock, free from any taint of contamination by a Trachyceratid group like *Cyrtopleurites.*

The family Haueritidae Smith (1927*a*) is then rejected in favour of Cyrtopleuritidae Diener (1925), and the genotype of *Hauerites,* namely *H. rarestriatus* (Hauer), is interpreted, as by Mojsisovics in 1893, on the evidence of its companion-species, *H. aeskulapii,* which more clearly reveals the affinities of the stock. Another form, *Cyrtopleurites distefanoi* Gemmellaro, also connects directly with *Hauerites ;* and, as Diener

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[1] The hypothetical genus *Pseudo-Hauerites* (Arthaber, 1911) has, of course, no standing, as already pointed out by Diener (1915*b*).

pointed out repeatedly, the external and internal characters of that genus were in favour of close genetic relations with *Cyrtopleurites*. The suture-line is similar to that of *Paratibetites* and only slightly more complex than that of *Drepanites* Mojsisovics (1893), which may look rather different at first sight on account of its Arpaditid earlier stages, but which reveals its Trachyceratid relationship with *Hauerites* in a general resemblance in the adult. *Drepanites*, however, develops a rounded body-chamber, not an increasingly narrower venter.

H. Family TIBETITIDAE Hyatt (1900).

The genus *Tibetites* Mojsisovics, 1893 (genotype : *T. ryalli* Mojsisovics, 1896*a*) was first envisaged as a sub-genus of *Cyrtopleurites*, above discussed, but in 1896 it was described as a separate genus, being more or less a Himalayan equivalent of the European *Cyrtopleurites*. The morphological agreement was described as extraordinarily great. The only difference, in fact, was said to be in the two rows of ventral clavi, or spirally elongated tubercles, which were plain in *Tibetites*, but fringed or notched in *Cyrtopleurites*. Now if this were the only real distinguishing character between the two genera, their separation into two distinct families would scarcely be justified. But Mojsisovics did not stress the differences in the suture-lines, as his sub-genera of *Tibetites* were based less on differences in the suture-lines than on morphological differences in the body-chambers.

Now *Tibetites* has a ceratitic suture-line with entire saddles, but the external saddle begins to break up so as to suggest the formation of an adventitious saddle. The appearance of this lobule in the external saddle of *Tibetites*, like the splitting-up of the same saddle in some Sirenitids (*Pseudosirenites*), indeed, was sufficient for Arthaber (1911) to claim affinity of these stocks with his heterogeneous family Carnitidae, a contention already rejected by Diener. All the same, the suture-line of *Tibetites* is clearly different from that of *Heraclites* on the one hand, and of *Cyrtopleurites* on the other.

Anatibetites Mojsisovics, 1896*a* (genotype : *A. kelvini* Mojsisovics, 1896*a*) scarcely differs in suture-line from *Tibetites* itself, but it was founded (as a sub-genus) on the ventral flattening of the body-chamber. Mojsisovics, in fact, stated that in consequence of the loss of the ventral tuberculation in the adult *Anatibetites*, the resemblance to *Heraclites* became so close that without knowledge of the differences in the suture-line the two genera could not be separated. Krumbeck (1913) doubted the significance of this morphological difference, but he must have misidentified a similar Timor example; for his *Neotibetites* is obviously already different on the chambered part. Moreover, Diener (1906*a*) redescribed *A. kelvini* from a rich assemblage of specimens[1] and added *A. hobsoni*, which completely justifies the retention of the genus *Anatibetites*.

Paratibetites Mojsisovics, 1896*a* (genotype: *P. bertrandi* Mojsisovics, 1896*a*) has a more complex suture-line than either *Tibetites* or *Anatibetites*, but there is the same outline. The frilling is slight in the Indian *P. geikiei*, with the tops of the saddles still entire, though less so than in the typical *P. bertrandi*. But in *P. wheeleri* Diener the external saddle is already didymitid, with an adventitious saddle developing from the median saddle in the external lobe. In the species of *Paratibetites* from Timor, the suture-line may be ceratitic, with the typical external saddle of *Tibetites* (e.g. *P. tornquisti* var. *timorensis* Welter), or ammonitic (e.g. *P. augustisellatus* var. *posterior* Welter), as in the Himalayan *P. wheeleri* already mentioned.

The genus *Neotibetites* Krumbeck, 1913 (genotype: *N. weteringi* Krumbeck, 1913) is based on a so-called "large" species, and to avoid future misunderstanding I may take the var. *medius* (Krumbeck's pl. viii, fig. 5) as representative, i.e. as genolectotype. The smaller example (fig. 6) shows the change from a bicrenate to a simply carinate venter, which is reminiscent of *Paratibetites*. But the suture-line is simple in all Krumbeck's varieties and does not differ essentially from that of *Tibetites* or *Anatibetites*. There is no need for any of the nomenclatorial changes suggested by Krumbeck, even if they were permitted by the Rules.

The genus *Metacarnites* Diener, 1908*a* (genotype: *M. footei* Diener, 1908*a*) is now also referred to the present family. Diener himself, in 1915 (*b*), admitted that his previous views concerning the derivation of *Metacarnites* from *Carnites* had been erroneous and that the striking resemblance between the genera was merely a case of homoeomorphy. The same author's revised opinion that *Metacarnites* was very closely allied to *Paratibetites* is here accepted, both genera having an

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[1] One of the duplicates is in the Collection, with some very fine Timor examples of *Paratibetites*.

oxynote shell in the adult and thus resembling each other externally as well as internally.

Pterotoceras Welter, 1915 (genotype: *P. arthaberi* Welter, 1915) is a more doubtful Tibetitid, not only because its suture-line is ceratitic, without the characteristic lobule in the external saddle, but because the type is said to be of Ladinian age. The inclusion, in the same genus, of the more highly ornamented forms of presumably higher horizons, is therefore open to question. Diener (1920*b*) thought that *Pterotoceras* and *Tibetites*, though probably closely related, might be traced back to a common root-form with ceratitic lobes. In any case, *Pterotoceras* was the earlier genus because it occurred in the Ladinian (?) in Timor, but only appeared in Europe at the Carnian-Norian border.

Morphologically, there is little difference between the two groups, except that in the earlier *P. arthaberi* the three rows of tubercles disappear before the end of the septate stage, whereas in the Feuerkogel forms described by Diener the umbilical tubercles become increasingly stronger. *P. clarissae* Diener even shows the median and ventro-lateral rows strongly increasing on the body-chamber. The Timor forms, described by Diener in 1923, apparently are of the same type. But since the suture-line of *P. abnorme* Diener is not only ammonitic but has an adventitious saddle which results from subdivision of the external lobe, not the external saddle, there cannot be genetic affinity with the presumed Ladinian *P. arthaberi*.

The genus **Dimorphotoceras** gen. nov. is thus now established for *Pterotoceras abnorme* Diener (1923 p. 212, pl. xv, fig.1) from the Norian of Timor, which is a more involute member of the group of *P. helminae* and *P. clarissae* Diener (1920*b*). Whereas, in the true *Pterotoceras*, as here restricted, the ornamentation develops from tuberculate to almost smooth, as already mentioned, with only the ventral clavi persisting, the new genus shows progressive increase of the lateral or umbilical tuberculation, or both, to the end. The suture-line also differs in having a wide external lobe with a large median saddle which in the typical *D. abnorme* produced adventitious saddles. In *Tibetites* a similar adventitious element appears on the external saddle, and the external lobe is narrow and small. Since, however, in *Paratibetites angustisellatus* Mojsisovics, var. *posterior* Welter, an adventitious saddle is developed between the external saddle and the median saddle of the external lobe, which itself is producing an adventitious offshoot, there seems to be no reason why *Dimorphotoceras* should not also be included in the present family.

The two Sicilian genera, *Palicites* Gemmellaro, 1904 (genotype : *P. mojsisovicsi* Gemmellaro, 1904) and *Mojsisovicsites* Gemmellaro, 1904 (genotype : *M. crassecostatus* Gemmellaro, 1904), are also included in the present family, but show specialization in yet different directions. In the former genus, both umbilical and ventro-lateral tubercles are retained to the body-chamber, but the small ventral rows disappear. In *Mojsisovicsites*, the two ventral and two ventro-lateral rows are well marked on the inner whorls, and there are no umbilical and no true median tubercles, but the bulges that replace the latter may persist even on the almost smooth and rounded body-chamber. The suture-lines of both genera are ceratitic, but in *Palicites* the incipient sub-division of the external saddle causes a distinct resemblance to the suture-lines of normal Tibetitids. In *Mojsisovicsites* the downward sweep of the almost effaced second lateral saddle is an unusual feature. This genus is well represented in the Collection, and its study, on the whole, supports the connection with Tibetitids already accepted in Zittel's 'Grundzüge' (1921), after Gemmellaro's own suggestion. There is no mention of these genera in J. P. Smith's (1913) revision in the second English edition.

Diener (1920*b*) thought that *Palicites* could not be separated from *Anatibetites*, but to me the differences in tuberculation and whorl-shape are very real, even if we overlook the slight difference in the external saddle.

A very doubtful genus is *Stikinoceras* McLearn, 1930 (genotype : *S. kerri* McLearn, 1930) which was based on a form with compressed, flattened whorls and a narrow, smooth venter with a thread-like keel. Unfortunately the illustration is very sketchy, with no sectional outline, and in the description there is at least one obvious error in referring to the first row of tubercles as being on the "umbilical" shoulder, instead of the ventro-lateral border. Nevertheless, the two rows of tubercles on each side of the flattened, smooth venter suggested resemblance to *Mojsisovicsites* and, with McLearn's claim that the two genera *Stikinoceras* and *Mojsisovicsites* should be referred to the same family, had to be seriously considered, however unexpected the comparison. The statement that the suture-line of *Stikinoceras* was simple may be assumed to refer to a ceratitic suture-line, comparable to that of *Mojsisovicsites*.

In 1937*a* McLearn amplified the description of *Stikinoceras* by stating that the longer of the ribs were thickened at the umbilical border to form incipient bullae, whereas the outer tubercles were somewhat clavate. McLearn at the same time described a second species, *S. robustum*, which had stouter and thicker whorls, and stronger and fewer costae than the genotype, *S. kerri*. The illustration, unfortunately, again is not accompanied by a peripheral view or a sectional outline, but the lateral ornamentaion of *S. robustum* is remarkably like that of *Palicites*. The comparison of *S. kerri* to *Mojsisovicsites*, then, was viewed from a different angle, and I abandoned all attempts to fit *Stikinoceras* into the Clionitidae, to which a chance remark by Diener (1905*a*) had enticed me. It is unfortunate that another incompletely known genus has to be added to the present family, but I have on a previous occasion (1933*b*) objected to the publication of such " provisional " accounts of new genera. When more reliable information becomes available, it may be possible to remove *Mojsisovicsites*, *Palicites* and *Stikinoceras* from the Tibetitidae.

1. Family BUCHITIDAE Hyatt (1900).

This family is based on the genus *Buchites* Mojsisovics, 1893 (genotype : *B. aldrovandii* Mojsisovics, 1893), and it was defined as including primitive forms, similar to Celtitidae, with smooth, elevated, venter and suture-lines that may be entire, ceratitic or ammonitic (brachyphyllic). It is true that Hyatt added that more specialized shells had a slight keel on the narrow venter ; but this wide interpretation of the family resulted in its being made a receptacle for a number of genera that did not fit into any other group, from the large, discoidal and involute *Thisbites* to the tricarinate *Jellinekites* and the trachyceratoid but keeled *Glyphidites*. Diener, who, after the great Mojsisovics, was the most experienced worker on Triassic ammonites, and like him accepted much of Hyatt's work, did not use the family Buchitidae, which was reduced to a sub-family in J. P. Smith (1913), and abandoned altogether in 1927(*a*). On the other hand, the genus *Ceratites* and the family Ceratitidae were extended more and more, especially in the German editions of Zittel's

Grundzüge (e.g. 1921), to cover a miscellaneous assortment of sub-genera and genera from the Anisian *Bukowskites* to the Norian *Heraclites*.

Diener's genus *Epiceratites* was to a smaller extent a similar collective group for forms, mostly dwarfed, which were obviously not true *Ceratites* and, in any case, of Carnian or Norian age, but could not conveniently be relegated to any one of the genera of the Buchitidae. It is therefore necessary to review both the family and the various genera that have not yet been attributed to any of the foregoing families.

Buchites itself is very similar to *Clionites*, especially the forms in which the ventral furrow tends to be lost ; but this was not a slow process, gradually affecting the inner as well as the outer whorls. On the contrary, while some small forms retained the ventral interruption of the costation, others developed evenly rounded venters with ribbing continuous across, and a still different group of forms acquired slenderer, more involute whorls with more narrowly arched peripheries. This last type is transitional to the typical forms of *Epiceratites* of the *elevatus* group, and the peripheral ribs still show the characteristic forward projection. In some, indeed, the ventral aspect is not unlike that of *Badiotites eryx* (p. 66), with which Frech (in Frech & Renz, 1908) had confused even the genotype of *Buchites*, i.e. *B. aldrovandii.* From these it is but a step to forms like *Epiceratites kerneri* (Mojsisovics), which are almost keeled, while others (*E. riezingeri* Mojsisovics sp. of the Norian) have the more trachyceratid aspect of *Dionites*, and seem as out of place in the genus *Epiceratites* as still more doubtful forms of Celtitid appearance.

Two of the forms listed by Diener as *Epiceratites* were transferred by Kutassy (1933) to the genus *Metatirolites* Mojsisovics, 1893 (genotype : *M. foliaceus* Dittmar, 1866). This was stated by Hyatt and Smith to be undoubtedly derived from the true *Tirolites* of the Lower Trias, but to me not even the Middle Triassic *T. pacificus* of the same authors is directly connected with *Metatirolites*. *T. pacificus*, in fact, was already stated in 1934 (Part IV, p. 359) to be probably a *Durgaites*. The genus *Metatirolites* differs from *Epiceratites* and *Buchites* chiefly in its wider periphery and more pronounced tuberculation, so that one of the species (*M. subpygmaeus* Mojsisovics) was even described as possibly a *Heraclites*.

The genus *Eremites* Mojsisovics, 1893 (genotype : *Trachyceras orientale* Mojsisovics, 1882) includes a second species

(*E. crassitesta* Dittmar sp.) that is very similar to *Buchites heriberti* Diener, but without umbilical nodes, according to a specimen from Mojsisovics's own collection (B.M., No. C. 5628), a second one (C. 7332) being a young *Monophyllites*. Hyatt included *Eremites* in the Clydonitinae, but there is little resemblance to *Clydonites* as understood by Mojsisovics, or to *Ectolcites*, the other two genera in Hyatt's sub-family. On the other hand, *Clionites haugi* Mojsisovics is another form in which Trachyceratid characters have become more or less completely effaced, which brings us back to those *Clionites*-like developments of the typical *Buchites*. Mojsisovics himself took *Eremites* to be a Trachyceratid, which is, of course, true, in a general way. This view was echoed by Haug (1894), who thought *Eremites*, like *Sandlingites* and *Clydonites*, to be an isolated group of no great importance. Nevertheless, *Eremites* is morphologically so different from the other two genera just mentioned that it cannot be classed in the same family.

The genus *Helictites* Mojsisovics, 1879*a* (genotype: *Ammonites geniculatus* Hauer, 1855*a*) was originally made to include a group, later (1893) separated as "*Polycyclus*" (now *Hannaoceras*). This is referred to below, under the family Choristoceratidae. It is obvious, therefore, that the two genera are somewhat similar; *Helictites*, however, has been restricted to forms differing from *Buchites* in the presence of straight ribs going across the venter without any interruption or forward projection. The species of *Helictites* described from Timor by Diener (1923) and Pakuckas (1928), increase the impression that even now *Helictites* includes a variety of different types that may at some future date be further sub-divided. Meanwhile, we include in the genus both the magnificent originals of *H. alemon* Mojsisovics and of *H. subalemon* Diener.

Another group of forms included in the family Buchitidae constitute the Norian genus *Phormedites* Mojsisovics, 1893 (genotype: *P. juvavicus* Mojsisovics, 1893), some of the species of which show resemblance not only to the forms of *Epiceratites* with almost a keel, but also the carinate stocks of the family Thisbitidae. Mojsisovics stressed the intimate connection of his second form of *Phormedites* with *Daphnites*, yet he included the latter as a sub-genus in *Arpadites*. Diener pointed out in 1920(*a*) that Mojsisovics's scheme was contradictory; for *Phormedites* was still considered to be a sub-genus of *Ceratites*, and could not well be linked with a sub-genus of *Arpadites* in a natural classification. Diener's way out of this dilemma was to treat them as separate genera, but that did not solve the problem of the families or even super-families, namely, Ceratitida on the one hand, and Trachyceratida on the other. In the classification here adopted, the affinity of *Buchites, Eremites Phormedites* and *Helictites* (e.g. *H. atalanta*) with *Clionites* and other Trachyceratida may be more apparent than in the case of the other genera ; and sometimes it is reduced to the general character of the suture-line with its characteristic, broad lateral lobe. The ideal of a genuine genetic classification is not yet attainable, and it must suffice to make our systematics workable. It has also to be reconciled with the existing nomenclature, given by a variety of predecessors whose outlook differed as their material was restricted or of only local interest.

The general affinity with the Trachyceratida is also believed to express itself in the genus *Martolites* Diener, 1906*b* (genotype : *M. kraffti* Diener, 1906), which is only doubtfully included here, since its author described it as being allied to the Celtitids and therefore the super-family Tropitida. To me, the nearest relations of *Martolites* seem to be with forms of *Helictites*, e.g. *H. canningi* Diener and *H.* sp. ind. ex aff. *beneckei* Mojsisovics in Pakuckas (1928). The latter has a ventral ridge rather than a furrow, but similar constrictions and inner whorls, whereas these are more tuberculate in *H. canningi*, so far as can be seen. The differences in the suture-line are probably more apparent than real, and in the case of the original *Helictites beneckei* to be trifling. The length of the body-chamber is unknown in *Martolites*, but so is that of the Timor form above referred to.

J. Family THISBITIDAE nov.

The genera now included in the family Thisbitidae, which were known in 1900, were referred to the family Buchitidae by Hyatt.[1] They probably represent the more specialized types of Hyatt, with slight keel on the venter, and they certainly connect more or less completely with the genus *Phormedites* of the Buchitidae. But the keel may become quite pronounced, and in the genus *Jellinekites* the periphery

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[1] The omission of *Thisbites* is, no doubt, due to a slip, but the omission was not rectified in 1913 in J. P. Smith's revision. In the German editions of the 'Grundzüge,' *Parathisbites* was omitted.

is even tricarinate. The separation of these keeled forms from Buchitidae, in which the periphery is smooth or merely elevated, is suggested for systematic convenience.

The genus *Thisbites* Mojsisovics, 1893 (genotype: *T. agricolae* Mojsisovics, 1893) itself is said to be confined to the Carnian, but Kutassy (1933) listed at least one species as Norian. Many of the Alpine species are dwarfed, but larger forms have been described from India and Timor. The Trachyceratid aspect of the periphery, with the low keel arising or fading out between the two rows of ventro-lateral tubercles, the occasional resemblance to Choristoceratids, the clydonitic or simple, ceratitic suture-line, all confirm the position of *Thisbites* and its allies in the classification here adopted. I do not consider that the Californian form described as *T. uhligi* by J. P. Smith (1927*a*) has anything to do with that Alpine species (represented in the Collection) or even the genus *Thisbites*; a glance at the periphery and its keel alone is sufficient to rouse doubts about the identification. Nor is the Japanese *T. orientalis* Shimizu (1930*c*) likely to belong to that genus. It was described as differing from all other species of *Thisbites* in its much coarser costation, but is too badly preserved.

The genus *Parathisbites* Mojsisovics, 1893 (genotype: *P. scaphitiformis* Hauer sp., 1855*a*) is based on a form which was first included by Mojsisovics in *Hungarites*, since it is not only keeled but has a ceratitic suture-line. In 1893 Mojsisovics recognized the close affinity between his *Parathisbites* and the genus *Phormedites*, which has the same lateral ornament, and is aptly described as a *Parathisbites* without the keel. The genus is represented by a Hallstatt example of the typical *P. scaphitiformis*, and among the species of *Thisbites* is one from the *Tropites* Limestone of Byans, labelled *T. meleagri* Mojsisovics, which appears to be a *Parathisbites*. Diener (1906*a*) thought that the only feature of sub-generic importance was the development—in *Parathisbites*—of "lappets" crossing the ventral keel and forming a direct continuation of the lateral ornament. This is well shown in Diener's (1906*a*) pl. xi, fig. 23*b*, but not in 22*b*, also compared to the typical *P. scaphitiformis*; and in view of its prominent keel and narrow umbilicus, I am including *Thisbites meleagri* Mojsisovics in *Parathisbites*, despite its denticulated first lateral lobe.

In the genus *Glyphidites* Mojsisovics, 1893 (genotype: *G.*

docens Mojsisovics, 1893) the Thisbitid keel is serrated and the falcoid ribbing is granular, as in *Clydonites* and *Sandlingites*. This produced a form of striking aspect which apparently has never been rediscovered, except in Sicily, whence Gemmellaro (1904) recorded an incomplete fragment as *G.* cf. *docens*. There is no reason to doubt Gemmellaro's identification.

The rather distinct genus *Jellinekites* Diener, 1906*a* (genotype: *J. barnardi* Diener, 1906*a*) is based on an extreme, tricarinate shell that might be taken to be a Tropitid, for reduced suture-lines are known in that family. The reference to Dinaritidae, of course, was meaningless and I was inclined to think that the comparison to *Thisbites* and *Parathisbites* was partly prompted by the presence of a short body-chamber, a character whose systematic value was much depreciated by Diener ten years later (1916*b*). Yet *Jellinekites hoveyi* Diener, which is connected with *J. barnardi* by an intermediate form, *J. saundersi*, and especially *J. dieneri* Pakuckas (1928), show such close affinity with *Phormedites* that any resemblance to Tropitids is soon found to be superficial. Even *Parathisbites* includes tuberculate species (*P. nodiger* Diener 1906*a*) which, however, only have one keel. In *J. dieneri* even the median keel is low and there are almost no accompanying grooves, while the umbilicus is fairly narrow, yet the generic attribution seems beyond doubt.

The Sicilian genus *Siculites* Gemmellaro, 1904 (genotype: *S. dolomiticus* Gemmellaro, 1904) is included here with doubt because it was compared to *Thisbites* already by its author. It has a simple, ceratitic suture-line and a slight keel, also constrictions, but a narrower umbilicus than the Sicilian *Thisbites*, described by the same author, except, perhaps, *T. bittneri*, which also has constrictions on the inner whorls. But the spiral striation of *S. turgidus* makes the reference of *Siculites* to the present family very doubtful.

K. Family NORIDISCITIDAE nov.

This family is established for the single form **Noridiscites** (gen. nov.) *viator* Mojsisovics sp. (1893, p. 410, pl. cxlii, fig. 2) which cannot be placed in any known genus. Its reference to a sub-family instead of a full family would therefore serve no useful purpose, for this subfamily similarly could not be attached to any known larger group. In retaining the family, however, in the super-family Trachyceratida, I am relying on the typical suture-line, with its deep lateral lobe, a feature that, as Arthaber (1914) has shown, is common to many of the younger ammonite tribes of the Carnian and Norian in which, as a rule, there was no room, beside the large external lobe, for more than one or two auxiliaries.

Ceratites viator was placed by Diener (1915*a*) in the genus *Epiceratites*, originally a heterogeneous assemblage (see p. 77) which is here reduced to the typical group of *E. elevatus*, but even so, has to accommodate some incompletely known species. There is no place for *C. viator* either in this genus, *Epiceratites*, or in the family Buchitidae. Externally, of course, the discoidal shape of *Noridiscites* and its truncated periphery are reminiscent of various Eotriassic stocks of no real affinity, such as *Ambites* Waagen ; and the fact that *Noridiscites* has a high, external lobe might suggest affinity with *Norites* or *Ananorites*, the reduction of the auxiliary elements of the suture-line being almost complete. The absence of any Carnian connecting-link between the Noritids and the Norian stock, here discussed, may not be decisive evidence against genetic connection, but there is also the absence of the ventro-peripheral ridges so typical of *Norites*, in addition to the umbilical ridge. Moreover, as Mojsisovics pointed out, the earlier whorls had the truncated, narrow, flat venter found in many Anisian *Ceratites ;* and it is only the persistence of this truncation to a large diameter that is a striking feature of *N. viator*, the holotype of which is still septate at 42 mm. diameter.

Since affinity of *Noridiscites* with Sageceratidae or Pinacoceratidae is ruled out by the suture-line, it can only be suggested that this genus is a special development of the persisting " *Dinarites-Ceratites* " root-stock that probably had given rise to various earlier, so-called cryptogenetic stocks. The Celtitids specialized in different directions and are not likely to have produced a discoidal form like *Noridiscites*. The length of its body-chamber is unknown, but probably did not exceed one-half to three-quarters of a whorl.

L.? Family DISTICHITIDAE Diener (1920).

Mojsisovics's division Distichitea, like his Heraclitea, was used in an irregular way as a group-, not a family-name ; yet Diener (1923) and Pakuckas (1928) ascribed the family to Mojsisovics. It is accepted, however, by most workers on ammonites. The family is inserted here, as customary, among the Trachyceratida, for the baffling resemblance in lateral ornamentation between *Distichites* and *Tropites* on the one hand, and *Ectolcites* and *Arietoceltites* on the other, is offset by the Norian age of the present family. It is here considered possible that Distichitidae arose from a Clionitid group, like *Californites*. There could, of course, be replacement of a keel by a groove, connected perhaps with a thickening of the test or other mechanical adjustment, and it is not of fundamental importance to the structure of the shell as a whole. Such a tentative adjustment was tried by *Schistophylloceras* among the Rhacophyllitidae of the Lower Lias ; and the sudden appearance of a channel within the ventral groove of *Euhoplites* of the Gault probably had a similar mechanical explanation. But it cannot be proved that the resemblance between *Distichites* and *Tropites* is more than accidental, that is, that the earlier *Tropites* gave rise to the later *Distichites* by loss of the keel.

In the genus *Distichites* Mojsisovics (1893), which has for genotype *D. megacanthus* Mojsisovics, 1893 (although Fischer, in 1879, quoted *D. celticus* as the only species), two groups were distinguished, namely, the *megacanthus*-group and the " group of *Distichites compressi*." The former was considered typical by Diener in 1915(*a*) ; and the year after, he proposed the genus *Paradistichites* Diener, 1916*e* (genotype : *Distichites ectolcitiformis* Diener, 1906*a*) for the second group. Perhaps a better example would have been *D. reynoldsi* Diener, which was described as the most conspicuous form of the group, being distinguished from all the European species by its peculiar ornamentation. The many Timor forms of *Distichites* described by Diener, in 1923, confirm the existence of these two separate groups, although they are connected by transitions.

Such transitions also occur to the genus *Ectolcites* Mojsisovics, 1893 (genotype : *E. pseudoaries* Mojsisovics, 1893) with typically undivided costae and a ceratitic suture-line. This last feature, however, may not always apply ; for Diener and Welter have described forms from the *Tropites* Limestone of Byans and Timor in which the saddles are not entire, as in the two Alpine species of Mojsisovics, but distinctly brachyphyllic. Also the external keels in some of the Indian species, like *E. hollandi* Diener, are extremely well formed, unlike Mojsisovics's original forms which have no ventral furrow on the inner whorls. Here again, it could be held that *Arietoceltites* Diener (p. 94) is strikingly like some forms included in *Ectolcites* (except the presence of a median keel) and there is not even a difference in age.

The examples of *Distichites* in the Collection include only one from Timor, and *D.* cf. *sollasii* Diener, and *D.* sp. (group of *D. megacanthus*) from the *Tropites* Limestone of Byans. From the latter deposit also comes an example of *Ectolcites duncani* Diener.

M. Family CHORISTOCERATIDAE Hyatt (1900).

The family-name, Orthopleuritidae, was used by Mojsisovics and Haug before Hyatt split the group up into the two families, Choristoceratidae and Cochloceratidae; these are here adopted, the former name, Orthopleuritidae, being in any case inadmissable by the Rules of Nomenclature. J. P. Smith, who in 1913 (in Zittel's 'Text-Book'), had retained the two groups, but reduced them to sub-families within the Ceratitidae, in 1927 (*a*) listed *Choristoceras* merely as a genus of Ceratitidae; he called it a degenerate, arrested genus, probably descended from "*Polycyclus*," whereas Mojsisovics had connected the earliest (and only Carnian) species he described, with the genus *Thisbites* Mojsisovics. J. P. Smith recorded the genus from California, after Clapp & Shimer (1911) had described a species from Vancouver Island, British Columbia. Both of Smith's species were described as loosely coiled, but ***not*** uncoiling, and they differ considerably from each other.

The genotype of *Choristoceras* Hauer (1865) is *Choristoceras marshi* Hauer (1865). Mojsisovics (1893) distinguished two groups, but they are connected by transitions, as was pointed out by Pompeckj (1895). Rather different and not even coiled in one plane, yet regarded as a possible development of "*Polycyclus*," is the genus *Peripleurites* Mojsisovics, 1893 (genotype: *P. roemeri* Mojsisovics, 1893). It was still listed as a sub-genus of *Choristoceras* by Kutassy (1933) and it is confined to a few species, which have only been found in the Alpine and Hungarian Upper Trias. It, however, clearly deserves to be ranked as a separate genus.

Hannaoceras Tomlin (1931) was introduced to replace *Smithoceras* Hanna (1924), which itself had been proposed in place of *Polycyclus* Mojsisovics (1893), also pre-occupied.[1]

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[1] My own name, "*Polysphinctoceras*" (Part IV, p. 198) was a MS. correction, made long before that part of this Catalogue appeared in print, and inadvertently left unchanged, in ignorance of Tomlin's correction.

The genotype of *Hannaoceras* is *Ammonites nasturtium* Dittmar (1866); the very evolute "*Polycyclus*" *nodifer* Hyatt & Smith (1905, p. 201, pl. xxxviii, figs. 1-18, as interpreted by No. C. 21908, and two topotypes from the collection of Prof. J. P. Smith) is sufficiently distinct from the type as well as the compressed forms of the *henseli* group to be separated, at least as a subgenus: **Sympolycyclus** nov. The suture-line may be clydonitic or sub-ceratitic in *Hannaoceras* and the genus passes up into the Norian. *H. ernesti* Mojsisovics, with flattened venter and faint tuberculation resembling that of *Eremites orientalis* Mojsisovics, is apparently not intermediate between *Hannaoceras* and *Sympolycyclus*, for in the latter the ventral groove (not confined to the earlier stages) fore-shadows the ornamentation of *Choristoceras*. There is more variation, however, in the Californian examples of *Hannaoceras* before me than in the Alpine *H. henseli* (Oppel). The Bosnian *H. senex* Diener sp. (1917*a*), without ornament in the adult and flattened sides, is apparently yet a different type.

One of the Californian examples of *Hannaoceras* was sectioned and was found to have a small protoconch (about ·3 mm.). The increase in coiling is fairly rapid, there being four-and-a-quarter whorls of air-chambers and three-quarters of a whorl of body-chamber at 14 mm. diameter. The siphuncle (of medium thickness) is still well away from the venter on the third whorl ; then the septa are destroyed until the final septum. Its funnel is not well shown, but may not be quite external, even then, as in other Trachyceratida. There are only about nine septa in the first whorl, up to the initial constriction.

One curious feature of *Hannaoceras* (even the compressed *H. henseli*) is that it resembles the globose *Leconteiceras*, in doubling its test at about 3 mm. diameter ; and the folds thereafter and their three layers are very similar, if less extreme than in *Leconteiceras*. The latter has been taken to be a Haloritid, as stated on p. 110, and it is perhaps nearer to *Lobites* (and *Coroceras*) than any other Tropitid, in shape, aperture, and even the bifid lateral lobe. But *Hannaoceras*, the type of which is the more globose "*Polycyclus*" *nasturtium*, has generally been included in the Ceratitida or the Trachyceratida, along with the other groups here adopted, although its connection with *Leconteiceras* may be at least as close. It is not impossible, therefore, that future investigators will refer that genus to the family Choristoceratidae, that is to say, the curious resemblance between *Hannaoceras* and *Leconteiceras* may not be so superficial as J. P. Smith thought.

The Norian genus *Rhabdoceras* Hauer, 1860 (genotype: *R. suessi* Hauer, 1860) was long represented by merely the type species and its var. *curvata* Mojsisovics, raised to specific rank by Jaworski (1922). The young stages of *R. suessi* have been studied by Janensch (1906), who seemed surprised that *Rhabdoceras*, after the two initial coiled whorls, suddenly became straight, without an intermediate *Choristoceras* stage. Such transitions, of course, are not now considered necessary to confirm the close relationship between *Choristoceras* and especially *Peripleurites* on the one hand, and *Rhabdoceras* on the other. Hyatt & Smith (1905) added another species (*R. russelli*) which differs in suture-line, notably the external lobe, which is much deeper than in *R. suessi* and especially in *Peripleurites roemeri*.

Apart from the commoner species of *Choristoceras* from the Alpine Koessen Beds, the Collection includes a slab of rock from Nuataus Tatu Anus, Timor, with several examples of *C.* cf. *ammonitiforme* (Gümbel) Welter, and a fragment of possibly a new species.

N. Family COCHLOCERATIDAE Hyatt (1900).

This family, also reduced to a sub-family in J. P. Smith's revision of Zittel's 'Text-Book' (1913), was later abandoned altogether and *Cochloceras*, with the sub-genus *Paracochloceras*, is now generally included in the family Ceratitidae. The family Cochloceratidae, however, is here adopted in Hyatt's sense, with the two sinistral genera *Cochloceras* Hauer, 1860 (genotype: *C. fischeri* Hauer, 1860) and *Paracochloceras* Mojsisovics, 1893 (genotype: *C.* (*P.*) *canaliculatum* Hauer) as independent genera. They are known only from the Alpine and Timor Norian.

Mojsisovics thought that there was neither a Triassic nor a pre-Triassic genus known that could be considered to be a direct fore-runner of *Cochloceras*. It does not seem necessary to look beyond the helicoid *Peripleurites roemeri* for such an ancestor.[1] While the reduction of the lobes from six to four

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[1] In 1937 (p. 508) I suggested derivation of *Cochloceras* from a normal ammonite (*Hannaoceras*), but it seems to me now that like the Turrilitids of the Cretaceous, *Cochloceras* also is derived from more loosely coiled ancestors, or at least, that they have a common root-form.

is not startling, considering the modification in the Cretaceous Turrilitids, the backward direction of the siphonal funnels (as in goniatites and Clymenids) is not borne out by Mojsisovics's figure. The one funnel shown in his fig. 12 (pl. cxxxvii), in fact, is pointing forwards, not backwards.

VII. Super-family TROPITIDA, Hyatt. 1900.

This corresponds to the Tropitoidea of Pakuckas (1928) who had recognized four families: Haloritidae, Tropitidae, Sibiritidae and Celtitidae, as originally established by Mojsisovics, and as here adopted, slightly re-arranged and with minor changes in the nomenclature. Hyatt (1900), it is true, had separated the Tropitida (with the two families Tropitidae and Haloritidae) in a different sub-order from the Celtitidae and Sibiritidae which he referred to the super-family Ceratitida. This is comprehensible; for both the Celtitidae and the Ceratitidae are probably derived from the Meekoceratida (or Lecanitida in Hyatt). But it may have seemed objectionable to those who still considered the length of the body-chamber a reliable systematic character. In any case, Hyatt's sub-orders are now completely superseded, as are the three groups into which Haug (1894) divided the Trachyostraca, including the Celtitidae. J. P. Smith (1913), in the second English edition of Zittel's 'Text-Book,' in fact, resumed the customary division of the Tropitidae into the four sub-families already mentioned, though his treatment of the Ammonoidea as a whole was not always an improvement on Hyatt. Mojsisovics's[1] latest grouping of the Tropitida into five families (Didymitidae has to be added to the four above cited) was then generally followed, but in reality the contents of J. P. Smith's four sub-families do not bear closer investigation, e.g. the inclusion of *Proteusites* and "*Margarites*" (already listed under Tropitinae) in the subfamily Celtitinae. J. P. Smith's later (1927*a*) treatment of the Tropitoidea was altogether theoretical. He traced the Tropitidae back to one species of the Carboniferous *Gastrioceras* and the Haloritidae (by way of *Acrochordiceras*) to another species of the same goniatite genus. On the other hand, he correctly excluded from Tropitidae the Lower

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[1] As adopted in Diener (1919), p. 341.

Triassic *Sibirites,* then taken to be "more likely a member of the Meekoceratidae," while, however, including *Metasibirites* in the Haloritidae.

Arthaber's (1911) classification, going back to even more remote goniatite ancestors for the Triassic ammonoids than J. P. Smith's, has been criticized already in Part IV. As emended by the latter author (1927*a*, p. 21; and 1932 pp. 26–30), we notice, for example, the wide separation of Celtitidae from the presumably allied Ceratitidae. In the present classification such separation is accidental and due partly to an attempt to retain priority of nomenclature, e.g. the use of Tropitida instead of the more logical name, Celtitida. Various other slight regroupings have already been adjusted in Part IV, but the five major divisions emerging from that reshuffle are again five of the six super-families (or sub-orders) here adopted. Trachyceratida were, however, included with the Ceratitida which is merely a matter of arrangement; for in 1914, J. P. Smith (p. 121) considered *Nevadites* to be a connecting link between the Trachyceratids and the *Ceratites* "of the group of *C. bosnensis*" (see p. 458, Part IV), a view still accepted in a general way.

The Tropitida are here sub-divided into the five families already recognized by Mojsisovics, and it is only because the number of genera has become unwieldy that the family Tropiceltitidae is now separated from them, and the two sub-families Sagenitinae and Episculitinae have been distinguished within the family Haloritidae. The name Sibiritidae also had to be changed to Metasibiritidae, in view of what was said in Part IV, p. 343, the true family Sibiritidae of Lower Triassic age being unrelated to the Upper Triassic genera here discussed.

A. Family TROPITIDAE Mojsisovics (1893), emend.

The typical genus of this keeled family, of course, is *Tropites* Mojsisovics (in Neumayr, 1875) itself (genotype: *Amm. subbullatus* Hauer, 1850) which is one of the most easily recognized of all Triassic ammonites, with its peculiar, cadicone whorl-shape and contracting final whorl. The flattened types which later became *Discotropites* Hyatt & Smith, 1905 (genotype: *Amm. sandlingensis* Hauer, 1850) were separated off from the bullate *Tropites* as early as 1879, but, unfortunately, they were given a wrong name (*Eutomoceras* Hyatt,

1877) by Mojsisovics and this caused confusion in geological literature for many years. This mis-use, by the great authority on Triassic ammonites, of the name of a Ceratitid genus for the flattened Tropitids may seem a small error to us now ; but as recently as 1938 Arabu fell a victim to this confusion, believed to have been straightened out long ago.

The following sub-genera were introduced by Mojsisovics in 1893 : *Anatropites*, for *Tropites spinosus* Mojsisovics (1893), including forms in which the small tubercles of the prominent umbilical edge are increased to real spines, at least on the inner whorls, while the whorl-shape on the whole is less extreme. *Paratropites* Mojsisovics, 1893 (type : *Tropites bidichotomus* Mojsisovics, 1893[1]) is characterized by laterally compressed, high, involute whorls and the similarity between the mature forms and the earlier stages. *Microtropites* Mojsisovics, 1893 (type : *Tropites galeolus* Mojsisovics, 1893) was established for dwarfed shells showing signs of degeneration, such as a tendency of the ornamentation to become obsolete, and of the body-chamber to leave the regular spiral and become contracted. Finally, *Paulotropites* Mojsisovics, 1893 (type : *Tropites labiatus* Mojsisovics, 1893) was introduced as a sub-genus of *Tropites* for the *labiati*, with the umbilical tubercles obsolescent and with paulostome constrictions on the body-chamber.

To these must be added *Gymnotropites* Hyatt & Smith, 1905 (type : *Paratropites americanus* Hyatt & Smith, 1905), which is distinguished by its smooth involute shells with narrow venters, but which is connected with *Paratropites* by transitions. Of these five sub-genera only *Paratropites* has been given generic rank, by Hyatt & Smith already in 1905, and by Diener in 1923 ; but *Gymnotropites* and *Paulotropites* are still regarded by most authors as its sub-genera, whereas *Anatropites* and *Microtropites* are included as sub-genera in *Tropites* itself. They are now all listed as of equal generic rank, partly because the " superiority " of some is largely numerical, partly because they are on a higher level than the many divisions now recognized by Smith (1927*a*) within *Tropites*, groups that may themselves some day be regarded as of sub-generic rank.

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[1] *Fide* Hyatt & Smith (1905), p. 53. They mentioned that *P. bidichotomus* was the first species described, but that *P. saturnus* (Dittmar) was the commonest and best-known species of the group and would make a better genotype, having probably been considered typical by the author, along with *P. sellai* Mojsisovics.

The genera so far discussed form a homogeneous assemblage and are recognized as closely related by their resemblance in fully-grown individuals, not by the recapitulation of a *Gastrioceras*-stage, as J. P. Smith (1932) contended. The globose young, in fact, before the keel appears, could not be definitely assigned to any particular family, as every worker on ammonites knows. *Tropites* may be attached to the evolute Middle Triassic *Tropigastrites* because the coronate inner whorls of a form like *T. trojanus* Smith, could be held to foreshadow the depressed and keeled types that were to become so numerous in the later Carnian. But there is not the convincing series of passage-forms which link, for example, that perfect homoeomorph of the Triassic *Tropites*, namely, the Sinemurian *Pseudotropites ultraliassicus* Canavari, with other " Arietitids " and finally with the uncarinate, smooth *Psiloceras* root-stock of the lowermost Lias, within the range of only two ammonite zones. Even that new Spitsbergen form of presumed Ladinian age, referred to on p. 144, is too involute to be an ancestral *Tropites*. But it shows how a *Tropites* keel could be developed in the young of any given stock, as the coronate whorl-shape of the young may appear in any stock at any time.

The seven genera above mentioned are well represented in the Collection, from Alpine and Sicilian localities, a few from India and Timor, and especially from California (Brock Mtn., Shasta County, P. Train coll.). Many of the specimens from the latter locality are still untrimmed, as broken out of the rock, and most of them are only roughly sorted, and none named, so far. But a selection of species from the same locality, and named by Prof. Smith himself, was presented to the Museum by Dr. Trechmann in 1920.

The family also includes the genus *Hoplotropites* Spath 1929 (= *Margarites* Mojsisovics, 1889) which has for genotype *Amm. jokelyi* Hauer, 1855*a* (*fide* Diener, 1915, p. 188). It is unfortunate that the well-known name *Margarites* had to be changed, but it was a homonym ; it was still-born, and according to the Rules cannot be brought to life. *Hoplotropites* has a more open umbilicus than the seven genera above listed, and there may be one, two or three rows of tubercles with varying degrees of prominence. An example of *H.* cf. *circumspinatus* (Mojsisovics) figured by Diener (1906*a*, pl. i, fig. 7) has an apparent ventral sulcus, as in *Distichites*. Since the dorsal area of the fragment retained the impression of the keel of the next inner whorl, there can be no doubt about the identification, but the specimen is of interest in connection with a suggestion made on p. 83 about the systematic value of ventral keels and furrows.[1]

Hoplotropites connects more or less directly with *Margaritropites* Diener, 1916*e* (genotype: *Anatropites margaritiformis* Diener, 1906*a*), in which the tubercles are very large and coarse. There is great resemblance to the unispinose forms of *Hoplotropites*, but the tubercles remain truly umbilical, not marginal tubercles. The furrows accompanying the sharp keel are very low.

The genus *Styrites* Mojsisovics, 1893 (genotype: *S. tropitiformis* Mojsisovics, 1893) may have been correctly interpreted by J. P. Smith as a degenerate Troptitid. The type is smooth, but has the appearance of a normal Tropititid, with excentrumbilication setting in; only its suture-line is extremely simple. Thus, Hyatt (1900), who interpreted *Styrites* as a Celtitid and classed it with *Tropiceltites*, may have been equally right. An examination of the Sicilian specimens of *Styrites*, *Tropites* and *Tropiceltites* in the Collection suggests that they are all very closely allied. Still other interpretations of *Styrites* have been offered. Broili (in Zittel's 'Grundzüge,' 1921, 1924) put *Styrites* in the Ceratitidae; Haug (1894) had it in Sibiritidae, which (as Metasibiritidae) is here, at least, included in the super-family **Tropitida**. The Tropitid keel of the examples in the Collection including such Alpine species as, e.g. *S. collegialis*, *S. subniger*, and *S. cristatus*, supports Mojsisovics's original classification of *Styrites* as a near ally of *Tropites*, although its suture-line is clydonitic.

Another not very typical genus of the present family is *Sibyllites* Mojsisovics, 1893 (genotype: *S. tenuispinatus* Mojsisovics, 1893) and this also, like *Styrites*, has been referred to Ceratitidae as well as to "Sibiritidae," but it has at least an ammonitic suture-line. The inner whorls of these evolute shells resemble *Hoplotropites*, but they have no keel. The venter only becomes acute at a later stage, and a blunt keel is formed on the outer whorl, often combined with a decline

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[1] The nucleus of a Californian *Paratropites* (diameter 10 mm.) shows a normal keel at the beginning of the outer whorl; then, presumably as the result of an injury, there follows a wide groove which gradually becomes narrower, and towards the end a renewed keel appears within the groove. At larger diameters this specimen probably would not have shown any difference from normal individuals.

in the ribbing. The suture-line is like that of *Hoplotropites*, which may justify retention of *Sibyllites* in the Tropitidae. Some species, however, like *S. gemmellaroi* Mojsisovics, with more of a real *Tropites* keel, greatly resemble *Tropiceltites*.

The genus *Timorotropites* Diener, 1916*e* (genotype: *Tropites dubiosus* Welter, 1914) is included here, although, as the latter author pointed out, it is a Tropitid of somewhat uncertain standing. It is as involute as *Microtropites* and has the ribbing and especially the spiral ornamentation of the typical *Tropites subbullatus*, but the keel does not appear until late in its ontogeny. The whole aspect suggests a Haloritid rather than a Tropitid, and the suture-line is more deeply sub-divided than in most Tropitids and comes nearer to that of *Jovites*. The form, in fact, may be taken to confirm the close affinity between the two families Tropitidae and Haloritidae, but it is a matter of taste to which of them it may be assigned. The cross-section given by Welter shows a very unusual umbilical " funnel," not at all like that of any other Tropitid in the narrower sense.

Pakuckas (1928) listed the genus *Waldthausenites* Welter (1914) among the Tropitidae, the only species of which was originally compared by its author to the Trachyceratid genus *Sirenites*. Diener had it in Tropitidae, on account of a distant resemblance to *Discotropites*; but the peculiar keel (recalling that of *Quenstedtoceras* developing out of the Callovian Cadoceratids) suggests reference to Haloritidae.

The internal structure of the Tropitidae may here be reviewed, though it does not throw much light on the hitherto unexplained problem of the sudden appearance of an enormous spate of these Tropitids in the Middle Carnian which so baffled Mojsisovics. It had been known that the siphuncle in *Tropites* was thick (one-third to one-quarter of the whorl-thickness) and that it was internal at first, not becoming external until after about three-and-a-half whorls, or even later. There is some variation in this respect, not only among five sections of *Tropites*, but between the latter and the compressed *Discotropites*. Their chief difference, however, is in the rate of increase of the spiral, the whorl-height in *Tropites* being 30 per cent., and, in *Discotropites*, 45 per cent. of the diameter (21·5 mm.). Both, then, have 13 septa on the outer whorl, but the thickness of the siphuncle in *Tropites* is still about one-sixth, and in *Discotropites sandlingensis* only about one-tenth, of the whorl-height. In a section of *Paratropites sellai*, however, at 4·5 mm. diameter, the thickness of the siphuncle is still a quarter of the whorl-height. The latter also shows the convexity of the septa (up to a diameter of 18 mm.) corresponding with that of five sections of *Tropites*; but this convexity is not pronounced on the inner whorls figured by Branco (1880) and the writer (Spath, 1933*a*). The differences in the number of septa in the last two and the other sections available are not considered of significance. In *Discotropites sandlingensis*, moreover, the long septa are biconvex, as in Trachyceratids. These observations, though not conclusive, may be compared with what is said below (p. 101) concerning the internal features of such presumed fore-runners of the Tropitids as *Columbites* and *Tropigastrites*.

B. Family TROPICELTITIDAE, nov.

The few genera here grouped as a separate unit have generally been classed with Tropitidae or, more frequently, Celtitidae, but their removal makes these two families less unwieldy. The very simple suture-lines of the smaller forms agree with those of the later Celtitids; the large *Arietoceltites* from India has a ceratitic lateral lobe, followed by a slender saddle, the margins of which might even be faintly serrated. But there is only one more lobe on the umbilical wall.

The genus *Tropiceltites* Mojsisovics, 1893 (genotype: *Clydonites costatus* Hauer, 1866) was restricted to the group of the *costati* by Mojsisovics himself, so that Diener (1915*a*) took that species to be the type. Hyatt & Smith (1905) had chosen as genotype *T. rotundus* Mojsisovics of the same group which happens to be the first species described; and although their selection has priority, I accept Diener's ruling as being in accordance with the original restriction. Mojsisovics's contention was that *Tropiceltites* is still close to *Tropites* and *Margarites*, though with loss of tubercles, and that the keel may be developed on a smooth venter, not sunk into it. The reference to Celtitids, however, favoured by Arthaber, could also be considered; only that author's own *Tropiceltites* from the Albanian Lower Trias, already discussed under *Pseudarniotites* (p. 9), is not here believed to have any connection with the Carnian forms under discussion.

The separation of two of Mojsisovics's three original groups of *Tropiceltites* as a sub-genus *Arnioceltites* leaves it open as to which species is to be considered the sub-genotype, either *T. laevis* or *T. arietitiformis* Mojsisovics. The creation of *Arietoceltites* by Diener (1916*e*), with *Tropiceltites arietitoides* Diener (1906*a*) as genotype, seems to settle the point in favour of *T. laevis* Mojsisovics (1893) as genotype of *Arnioceltites*. The latter thus includes the forms with obsolescent lateral ribbing, while *Arietoceltites* covers the species with numerous volutions and " arietitoid," i.e. *Arnioceras*-like, ribbing and deep furrows accompanying the ventral keel.

So far, then, the three groups of Mojsisovics's original *Tropiceltites* seem settled, at least nomenclatorially. *Tropiceltites* itself, restricted to the *costatus* group, may be interpreted as including forms with the fine, *Thisbites*-like ribbing of that species on the one hand, merging by way of intermediate types like *T. subgeometricus* and *T. adjunctus* into the more coarsely and distantly ribbed *T. rotundus* on the other. The Collection does not contain more than about a dozen examples, mostly from Mojsisovics's own cabinet ; but among them is *T. raimundi* Mojsisovics, with spinose inner whorls, changing to costate and finally more or less smooth ; and this species is not the only one that has a real *Tropites*-keel, not just a carinate venter. Again, *T. inflatocostatus* Mojsisovics (Nos. C. 6331*a*, *b*) is almost a *Hoplotropites*, except for its later stages. According to its author, this represents the original stock, still close to *Tropites*, whereas in the more advanced forms of *Tropiceltites* the spinose stage is pushed back to the earliest stages.

The " total absence of spines " and the " absence of keel-furrows," of which Hyatt & Smith spoke, are thus not exactly characteristics of the *costatus* group ; and there are still other forms, e.g. *T. astragalus*, which is transitional to *Arnioceltites*, or *T. suavicostatus*, which is transitional to *Styrites*. Although the suture-line is unknown in some of the species, *Tropiceltites*, while still rather comprehensive, may then be accepted as a fairly compact assemblage.

Arnioceltites, comprising only three distinct species, is still more homogeneous, but it is not here considered to be a subgenus of *Tropiceltites* any more than *Arietoceltites*. One of the three species of *Arnioceltites* (*A. caducus* Dittmar sp.) was recorded from California as *Tropiceltites* (Smith, 1927*a*), but although the American specimens were described as being " exactly like the figures and descriptions given by Mojsisovics," the writer cannot accept the identification. The species, however, helps in the interpretation of *Tornquistites* as a degenerate Tropiceltitid.

Arietoceltites is also a fairly uniform group, and although one or two species with the furrows fainter than usual may be transitional to other Tropitids, and although *A. multispiratus* could be considered to lead to the tuberculate *Tritropidoceras*, the small Alpine forms seem to be congeneric with the large Indian genotype of *Arietoceltites*, already mentioned.

The genus *Tritropidoceras* Schenk, 1935 (genotype: *T. packardi* Schenk, 1935), with a curious resemblance to the Bajocian genus *Haplopleuroceras* Buckman, is probably closer to *Arietoceltites*, and especially *A. multispiratus* Mojsisovics, than to the true Tropitidae, as here restricted. It developed tubercles at the inner end and two near the outer end of the ribs, as in certain *Hoplotropites*. These, however, are never serpenticones, like the flattened *Tritropidoceras*, and they lack the three prominent keels. The suture-line, as figured by Schenk, is simple, but in the specimen in the Museum (No. C. 35932) referred to by Schenk, it can be seen that the external saddle has a much more slender top. Since the suture-line of the Indian *Arietoceltites* is at least ceratitic, if not ammonitic, there is no reason why *Tritropidoceras* should not also be included in the family Tropiceltitidae.

Haidingerites Mojsisovics, 1893 (genotype: *H. acutinodus* Hauer sp., 1860) is more doubtful, but included here because a crested periphery is generally developed in keeled stocks, e.g. Oppelidae; and even *Meneghiniceras* is a development of, or at least a parallel stock with, *Harpophylloceras* (e.g. the keeled *Rhacophyllites eximius* Hauer sp.). The unique type of *Haidingerites* is too far removed in time from the keeled Celtitids, like *Tropigastrites*, to be considered a degenerate offshoot of the restricted family Celtitidae. *Haidingerites* had been grouped with it, for example, by Hyatt (1900), who, like other authors, accepted Mojsisovics's association of *Haidingerites* with *Tropiceltites* (*Arnioceltites*). The inclusion in the present family thus only reflects the change in nomenclature.

Tornquistites Hyatt & Smith, 1905 (genotype: *T. evolutus* Hyatt & Smith, 1905, p. 60, pl. xxxii, figs. 11–21) is also included here only with doubt. It has a clydonitic suture-line and loose coiling, and it was interpreted by J. P. Smith as a degenerate Tropitid, possibly on account of the keeled

"*Styrites*-like" younger stages. But it is difficult to see how it can be "reversionary to ancestral types," if Tropitids are "Triassic Gastrioceratea." Four examples of *Tornquistites obolinus* (*non* Dittmar) in the Collection, named by J. P. Smith himself, are keeled to a diameter of between 10–14 mm., and therefore have nothing to do with the true *Amm. obolinus*, which is here taken to be a compressed *Episculites* (p. 114), as Mojsisovics believed. The keel, however, suggests affinity of *Tornquistites* with the less degenerate *Arnioceltites*, rather than *Styrites*. It is probable, in fact, that the Californian *Tropiceltites* (*Arnioceltites*) *caducus*, already cited, is a transition to *Tornquistites*, with more affinity to the other two American species of that genus than to any European *Arnioceltites*. In *T. evolutus* the keel is confined to a very early stage and the ribbing is lost completely, so that it is the most degenerate of the forms of *Tornquistites*. On account of the keel, that genus can be well kept distinct from *Episculites* and other degenerate Haloritids.

c. Family CELTITIDAE Mojsisovics (1893), emend.

The genus *Celtites* Mojsisovics (1882), it may be recalled, was first established for the two groups of *C. floriani* and *C. epolensis*, and while the first species was somewhat doubtful (as the length of its body-chamber was unknown) the second group was included in *Celtites* "not without hesitation," as the suture-line of *C. epolensis* (which had only four years before been referred to *Trachyceras*) was unknown. In 1888(*b*), and 1893 Mojsisovics restricted *Celtites* to *C. epolensis*, since the *floriani*-group, now forming the genus *Danubites*, had in the meantime been found to have a short body-chamber. Hyatt (1900) nevertheless included both the macrodome *Celtites* and the microdome *Danubites* (= "*Florianites*") in one family Celtitidae, in the super-family Ceratitida.

There is, thus, no doubt about the genotype of *Celtites*, which is important, as the genus has had the most widely different interpretations since Waagen (1895) entirely misrepresented it when including in it certain Lower Triassic forms from the Salt Range. The range of *Celtites* is even now given as Lower to Upper Triassic, which is wrong, whereas the usual definition of the genus or family ("including loosely coiled forms with long body-chambers and simple suture-lines") is somewhat too elastic.

The age of *C. epolensis* Mojsisovics is Ladinian ; and several (unnamed) examples in the Klipstein Collection, in the characteristic mode of preservation, but perhaps differing slightly among themselves, have as their most striking feature, at least of the inner whorls, the prorsiradiate ribbing. In the presumed descendant of *C. epolensis*, the small Carnian *C. klipsteini* d'Orbigny sp. (= *Goniatites buchii* Klipstein, *non* de Verneuil) the coiling was said to be more rapid, but the costation is of a different type, and Mojsisovics, indeed, put *C.* " *buchii* " into another group of *Celtites* from that of the genotype, *C. epolensis*.

There were eight examples of *C.* " *buchii* " in the Klipstein Collection,[1] probably including the holotype (pl. viii, figs. 11*a–c*) ; but, being pyritic, they have suffered considerably from decomposition. Two must have been lost early, because Crick only mounted six on a tablet at the time of registration (No. 36005), and now two more are entirely decomposed, and one which is still intact is beginning to break up. The only complete specimen, with two-fifths of the outer whorl belonging to the body-chamber (at 10 mm. diameter), has the typical suture-line of *C.* " *buchii*," but cannot be the same species, as it has minute tubercles at the inner and outer ends of the ribs. These are also more closely spaced and weaker than in two typical septate fragments which could have been portions of the holotype. They agree with Mojsisovics's fig. 7, and the inner whorls of his fig. 9 (pl. xxx), the original figure in Klipstein having been enlarged about × 2. These two fragments well show the external and internal suture-lines, as drawn by Klipstein,[2] but with a deeper internal lobe, though, apparently, not quite so deep as in Mojsisovics's figure. Finally, one body-chamber fragment shows approximation of the ribbing, as on the last whorl of Mojsisovics's fig. 9.

The tuberculate form, above mentioned as one of the originals of Klipstein's *Goniatites buchii*, shows some resemblance to an unnamed Hallstatt specimen in the Museum (No. C. 1713), which may be *C. sublaevis* Mojsisovics. That

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[1] The writer has a specimen labelled *C. buchi*, but possibly belonging to *Goniatites rosthornii* Klipstein, purchased from Krantz in Bonn many years ago, which is also marked ex " Coll. v. Klipstein." Another *Goniatites buchii*, labelled thus by the author himself, is in the J. E. Lee Collection (B.M. No. C. 1483). This happens to be a very small Trachyceratid.

[2] Serration of the principal lobe is just indicated. Laube's fig. 6 (pl. xxxvii) is wrong in showing the umbilical lobe in the side-views.

species was included in the group of the *acutoplicati* by Mojsisovics, together with *C. klipsteini* and species like *C. steindachneri*[1] and *C. faustus*. These are apparently close to *C. klipsteini*, whereas *C. emilii* and *C. theresiae*, perhaps also *C. subhumilis* Mojsisovics, are less obviously related to the *epolensis* group or the true *Celtites* which has closer relations with certain Middle Triassic forms referred to the genus *Tropigastrites*, as will be shown below. In the circumstances a new name becomes necessary for the " *buchii* "-group, and I propose **Orthoceltites** gen nov. (genotype: *Goniatites buchii* Klipstein, *non* de Verneuil, 1843, p. 137, pl. viii, fig. 11 = *Aganides klipsteini* d'Orbigny, 1850). This genus is not the equivalent of Mojsisovics's group of *Celtites acutoplicati*, because forms like *C. paucicostatus* Mojsisovics may not belong to *Orthoceltites*, whereas some species of the *multispirati*, like *C. laubei* or *C. gracilis* Mojsisovics, could be referable to that genus, if suture-line and costation agree. Unfortunately, these forms are not represented in the Collection, likewise many other species of *Celtites*, e.g. those described by Diener in 1917*a* and 1921.

Now, according to J. P. Smith, *C. epolensis*, the genotype, is apparently most nearly related to *C. polygyratus* Smith, which, in its turn, was stated to be close to *C. gabbi* Smith, and therefore to the genus *Tropigastrites*. An examination of specimens of these species, labelled by Prof. Smith himself, and especially of a large and still unnamed series of Nevada specimens from the P. Train Collection, confirms his opinion. But, since the suture-line of *C. epolensis* is still unknown, the resemblance is confined to the similarly prorsiradiate ribbing which is much less sharp and fine in the American forms. Smith left these two species in " *Celtites* " because they differed from *Tropigastrites* in their " goniatitic suture-line " ; but the only suture-line figured (1914, pl. xx, fig. 8*a*) is too immature to be of any use, except for Smith's own recapitulatory theories. These also made him refer to the Lower Triassic genus *Columbites* two ordinary forms of " *Celtites*" or *Tropigastrites* (*T. plicatulus* and *T. humboldtensis*), although they differ entirely in ornamentation.

The genus *Tropigastrites* Smith, 1914 (genotype: *T. trojanus* Smith, 1914) was created for a species that was

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[1] The American dwarf-form attached to this species by J. P. Smith (1927*a*) has a greatly reduced suture-line, with an undivided external lobe, almost as in *Paraganides* or the Devonian *Anarcestes*.

stated to have a strong resemblance to *Danubites dritarashtra* Diener. The principal difference from the "apparently nearly allied" *Tropigastrites trojanus* was believed to be the less broad whorl-shape and the weakness of the umbilical ribs in the Indian species. Yet Smith never mentioned that the genus *Pseudodanubites* had been established for *D. dritarashtra* by Hyatt, who may have interpreted it wrongly by including it in the Ptychitidae, but who had it at least in the same sub-order as the Celtitidae, the Ceratitidae and the ancestral Meekoceratidae. I referred the genus *Pseudodanubites* to Celtitidae in Part IV (p. 127), and am now including it in the Danubitidae (p. 14), not then separated. But in spite of a difference in the length of the body-chamber and a slightly different suture-line, the two genera, *Pseudodanubites* and *Tropigastrites*, are not so widely distinct as their reference to separate super-families would suggest.

In his summary-diagnosis of *T. trojanus* Smith pointed out that the suture-line was "weakly ammonitic." This feature is more distinct in other species of *Tropigastrites*, including the European *T. neumayri* (Mojsisovics). The serration of the first lateral lobe may be continued all the way up the external saddle, but the incisions may reach only half-way up on the siphonal side of that saddle. These proportions are reversed on the first lateral saddle, so that the small second lateral lobe has only four teeth ; what is visible of the umbilical lobe has merely two. This does not agree with the suture-line represented in Smith's fig. 9 (pl. xvii) which, moreover, has the external lobe only as deep as the first lateral, whereas in the suture-line of a magnificent Bosnian specimen of *T. neumayri*, var. *crasseplicata* (Mojsisovics), in the Museum (No. C. 20342) the external lobe is about twice as deep.

This example is septate to 75 mm. diameter and has the last nine septa rather approximate, but irregularly spaced. The next six septa are more distant, but it is only the remaining six septa of the early part of the outer whorl that are fairly widely spaced, though not so distant as in *T. edithae* Mojsisovics, or in the Danubitidae. Allowing for two more, now covered by the beginning of the body-chamber (and the test), this would make a total of 23 septa for the last wholly septate whorl, at 75 mm. diameter. In one of the American specimens sectioned, however, there are only 9 septa at 21 mm., and in another, 12 septa at 8 mm. diameter (end of the septate stage) and the last two are very slightly approximating.

Arthaber (1911) pointed out that the possession of long air-chambers, once considered a characteristic of *Celtites*, applied only to the *floriani*-group (i.e. the genus *Danubites*) and was rarely found in *Celtites*, but this obviously does not apply to *Tropigastrites*.

The Californian species of *Tropigastrites*, described by Smith, comprise a variety of strongly or feebly ribbed species, from the depressed genotype to the compressed *T. obliterans*; and I can see no reason for separating from them the two Anisian species of "*Columbites*" already referred to. These have the typical prorsiradiate ribbing, only slightly more oblique than in, e.g. "*Celtites*" *polygyratus*, and the suture-line is the same, though it also resembles that of the true, Lower Triassic *Columbites*, with its entirely different inner whorls. The peripheries of the American forms vary greatly from just broadly or narrowly arched to fastigate and bluntly or sharply keeled.

One type Smith did not figure, at least as *Tropigastrites*, is indistinguishable from the Bosnian *Sibyllites planorbis* Hauer. The original *S. louderbacki* Hyatt & Smith, it is true, differed chiefly in its greater whorl-thickness, but the Nevada form in the Collection (No. C. 40612), showing perfect agreement with typical examples of *S. planorbis*, may be the same species as that figured by Smith as *Gymnites* (*Anagymnites*) *acutus* Hauer. Since the suture-line of the American form was unknown and its preservation not very good, Smith admitted that the identification was doubtful; and, of course, there is no reason why the species should not be found in the Anisian of Nevada. The description of another form, however, as *Gymnites* (*Anagymnites*) *rosenbergi* Smith, is certainly wrong, for its suture-line is not in the least like that of a Gymnitid. Moreover, it shows a suspicious resemblance to that of *Tropigastrites rothpletzi* Smith (1914, p. 31, pl. xix, figs. 1–3) and the species may have been separated from its true companions because its inner whorls did not fit into that alleged "perfect genetic series from *Gastrioceras* to *Tropites*."

Thin sections were prepared of many of these Nevada forms, as there are numerous duplicates, and it was hoped to find at least some Tropitid characters. Celtitidae, however, being the most primitive of the Tropitoidea and *Tropigastrites*, according to its author, coming practically within the limits of *Celtites*, the siphuncle was found to be external from the start, or at least, very nearly external (in the second whorl of one defective section). The investigation proved somewhat inconclusive because the preservation of these Nevada forms, in a coarsely crystalline matrix, is not favourable to section-cutting, and the inner whorls are often displaced. On the whole the slides of *Tropigastrites* are similar to those equally imperfect sections of *Pseudaplococeras*, referred to on p. 35. These Anisian forms, described as *Lecanites* by Smith, are very common in the same hand specimens as the examples of *Tropigastrites*, but the costation of the latter is the obvious distinction.

Only two of the sections of *Tropigastrites* available showed a small protoconch (not measurable). The siphuncle is fairly thick as in *Pseudaplococeras* ; but it is only in *Celtites polygyratus* Smith, already referred to, that a really thick siphuncle is seen. It has a thickness of .4 mm. where the whorl-height is 2·4 mm., and ·2 mm. (or 25 per cent. of the height) in the third whorl, as in Tropitids, but it is external. The septation has already been mentioned as being irregular and often distant, as in the Danubitidae or in sections of *Glyptophiceras*.[1] There are only 8–9 septa in each of the first three whorls, and the short funnels are already directed forwards where first seen (at just over 2 mm. diameter). *Columbites*, which was believed by Smith to be the direct ancestor of *Tropigastrites*, is rather different. At least a section of *Columbites parisianus* Hyatt & Smith, from Idaho has the funnels directed backwards to a diameter of 15 mm., but the siphuncle, with a thickness of 20 per cent. of the whorl-height, is firmly established at the venter at 5 mm. The convex septa are comparatively distant ; there are only ten in the second whorl, and the same number still at 9 mm. diameter. On the other hand, in *Subcolumbites europaeus* (Arthaber) the slow coiling and the low whorls (22·5 per cent. at 20 mm. diameter) as well as the convexity of the septa are still more striking. The central part of the section shows an elliptical shape, and is not well preserved and partly displaced, but it has a thick, centro-ventran siphuncle that does not become external until the third whorl, while the conspicuous, long funnels are directed backwards and remain so to the very end of the septate stage (at 17 mm. diameter). It has an altogether more ancient

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[1] One of these shows only six septa on each of the first two whorls, after the initial constriction, that is actually on the second and third whorls.

appearance, recalling Permian types, in spite of the wandering siphuncle of its earliest whorls.

The fastigate *Sibyllites planorbis* Hauer, represented in the Collection by a number of specimens from Bosnia and Montenegro, has been referred to the genus *Japonites*, but shows neither its suture-line nor its ornamentation. It is very similar to *Gymnites acutus* Hauer, and some large examples in the Collection which do not show the characteristic suture-line (see p. 170) cannot be definitely identified. A new name is desirable for the *planorbis* group, which, at larger diameters, resembles *Anagymnites* more than *Tropigastrites*. I would propose the new genus **Tropigymnites**, gen. nov. (genotype: *Sibyllites planorbis* Hauer, 1896, p. 271, pl. xii, figs. 7–8). The similar Himalayan *Japonites chandra* Diener is less compressed and remains uncarinate to a late stage, but it is apparently not a *Japonites*, like the strongly-ribbed type of that genus, *J. planiplicatus* (Mojsisovics) or *J. raphaelis zojae* (Tommasi). Another form referable to *Tropigymnites* is *Japonites crnogorensis* Salopek, the suture-line of which is already much like that of the Indian *J. sugriva* Diener.

The small *Japonites ganghoferi* Reis (1901) is another interesting form of *Tropigymnites*, having the shape and typical suture-line of *T. planorbis*. In 1907, however, Reis considered that his identification required emendation, evidently as the result of an observation in the "Lethaea" that *Japonites* should be made a sub-genus of *Flemingites*. Thus, not only Reis's own *J. ganghoferi* and a form he previously described as ? *Gymnites spiratus*, but even Hauer's *S. planorbis* were cited as *Flemingites*. It is scarcely necessary to point out that there is not the slightest justification for connecting the Anisian genera just discussed with the Lower Triassic *Flemingites*.

The remaining Celtitids include first of all the group of the *annulati* of Mojsisovics, for which he created the sub-genus *Cycloceltites* Mojsisovics, 1893 (genotype: *C. annulatus* Mojsisovics, 1893), now raised to generic rank on account of the doubtful status of *Celtites* itself. They are characterized by having their fine and close ribbing continuous across the venter, except in the young. The isolated Norian *C. julianus* Mojsisovics does not seem to differ greatly from the young of the Carnian *Cycloceltites*.

Other groups separated from the original *Celtites* are *Otoceltites* Diener, 1916*e* (genotype: *C. perauritus* Diener, 1908*a*) and *Indoceltites* Diener, 1919 (genotype : *C. trigonalis* Diener, 1908*a*). The former, of Ladinian age, has no connection with the Norian *Cycloceltites auritus* (Mojsisovics). The two or three curious flares of its unique type-specimen are distinct from the regular paulostome ribs of *Cycloceltites* and, with the temporary cessation of ribbing, suggest some abnormality. *Otoceltites* again would not be accepted as a distinct genus if it could safely be attached to some other genus as a sub-genus. It has a goniatitic suture-line, like the second genus mentioned, *Indoceltites*, which is also of Ladinian age and which is based on another form with a very long body-chamber. The trigonal coiling of *I. trigonalis* is reminiscent of that of the Upper Devonian *Clymenia* (*Soliclymenia*) *paradoxa* Münster sp. (see Schindewolf, 1937, pl. i, figs. 4, 6–8), and may or may not be pathological, but the faint ornamentation is confined to the apertural end of the outer whorl.

The apparently more typical *Celtites laevidorsatus* (Hauer) leads to the rather specialized *C. rectangularis* (Hauer), also of Carnian age, and they form another group raised to generic rank, since it cannot well be made a sub-genus of the restricted *Celtites*. It may be given the name **Coeloceltites**, gen. nov. (genotype : *Amm. rectangularis* Hauer, 1860, p. 136, pl. iii, figs. 7–8). This may be defined as including Celtitidae with flattened sides and venter, the latter provided with longitudinal striation and tending to become concave, bordered by two raised and subtuberculate ventro-lateral edges. Suture-line presumably clydonitic ; body-chamber at least one whorl.

Whether such peculiarly ornamented species as *C. conifer* and *C. laevior* Diener (1917*a*), or the *Lecanites*-like *C. laevissimus* and *C. ottiliae* Diener (1920*c*) belong to yet different groups cannot now be established. In any case, *C. wittenburgi* Diener (1921), with tuberculate ventro-lateral edges, and a faint median keel on the periphery, does not belong here. It may not be a typical *Epiceratites*, but it is clearly out of place in the family Celtitidae.

D. Family METASIBIRITIDAE, nov.

The family Sibiritidae, of Lower Triassic age, was dealt with in Part IV (p. 343) and it was stated that the Upper Triassic genera, *Metasibirites* and *Thetidites*, were believed to be entirely independent developments, as suggested already by von Krafft (in v. Krafft & Diener, 1909).

Metasibirites Mojsisovics, 1896*a* (genotype: *Ammonites spinescens* Hauer, 1855*a*) was said to resemble the Lower Triassic *Sibirites pretiosus* Mojsisovics, but this resemblance is believed to be as superficial as Steinmann's comparison of *Sibirites* with the Bajocian *Zigzagiceras zigzag* (d'Orbigny). The genotype of *Metasibirites* is a rather advanced species; *M. annulosus* is only costate and typically untuberculate, but varieties may show tuberculation which is umbilical. *M. crassus* has an almost *Parkinsonia*-like venter and there may be constrictions and paulostome ribs, but the periphery is smooth in the young. In the Himalayan *S.* (? *Metasibirites*) *philippii* Diener the umbilicus is still wider, and the resemblance to *Cycloceltites* is considerable. As *Metasibirites* is exclusively Norian, it is believed to be a development of *Celtitidae* and to have no connection whatever with the Lower Triassic Sibiritidae.

In the genus *Thetidites* Mojsisovics, 1896*a* (genotype: *T. huxleyi* Mojsisovics, 1896*a*), also of Norian age, the bifurcation of the ribs occurs at marginal spines, not at the lower portion of the lateral parts (often quite near the umbilical margin) as in *Metasibirites*. The Timor species of *Thetidites*, figured by Diener in 1923, confirm that the genus is more than a mere sub-genus of *Metasibirites*, as Diener held in 1915(*a*). They also show how the latter genus had been misinterpreted by Smith, and they confirm the independence of the present family from Haloritidae. The reference by Mojsisovics of the Carnian *Miltites*, discussed under Haloritidae, to the present family, and its resemblance to *Tardeceras*, also of Carnian age, may thus be of significance.

Metasibirites was wrongly taken by Smith to cover the genus *Tardeceras* Hyatt & Smith, 1905 (established for the Californian *T. parvum* Hyatt & Smith). In 1927(*a*) J. P. Smith stated that *Tardeceras* only included the compressed forms of this group, but the depressed forms of the same group then figured are even less closely comparable to the non-American forms. Another species of this "*Metasibirites*" was even included in the genus *Tropiceltites* (*T. frechi* Hyatt & Smith). Both are degenerate Haloritids, and, in my opinion, are quite distinct from the true *Metasibirites*, as interpreted by Mojsisovics and Diener. There are many specimens of these *Tardeceras* from California in the Collection, both compressed and inflated, and it is clear that J. P. Smith misinterpreted the genus *Metasibirites*. This explains not only his inclusion of the misnamed *Metasibirites* in the Haloritidae, and his discarding of the whole family "Sibiritidae" (for the Upper Triassic forms), but his reference to such Tropitids as Gemmellaro's *Styrites tropitoides* or *Tropites aloysii* as probably forms of "*Metasibirites*."

It becomes necessary, therefore, to reinstate *Tardeceras* Hyatt & Smith to cover the American dwarf Haloritids and the larger example of the genotype, *T. parvum*, figured by J. P. Smith (1927*a*, pl. lx, figs. 31–32), shows that it differs from Smith's "*Metasibirites*" (first *Tropiceltites*) merely in the less robust ribbing. The umbilicus is comparatively small in all these forms, as distinct from the true *Metasibirites*.

E. Family HALORITIDAE Haug (1894).

This family was first introduced in 1893, as a sub-family of Tropitidae, but it was soon raised to family rank by Haug (1894), Mojsisovics (1896*a* and 1899) Hyatt (1900) and Diener (1906*a*).[1] It included the genera *Halorites* Mojsisovics, 1878 (genotype : *H. ramsaueri* (Quenstedt) Hauer sp., 1846) and *Juvavites* Mojsisovics, 1879*a* (genotype : *J. ehrlichi* Hauer sp., 1855*a*). The two sub-genera recognized by Mojsisovics in *Halorites* are now accepted as independent genera ; for *Homerites* Mojsisovics, 1893 (genotype : *H. semiglobosus* Hauer sp., 1855*a*) had been listed as such by Diener in his 'Catalogue' (1915*a*), though not in later publications, nor in Kutassy (1933). The other genus, *Jovites* Mojsisovics (genotype : *Tropites dacus* Mojsisovics, 1875), was recognized as a separate genus by its author himself (1896*a* and 1899), by Gemmellaro (1904), and by Diener (1915*a*) ; but it also was again reduced to sub-generic rank by the latter author in 1920. J. P. Smith (1927*a*) created the sub-genus *Bacchites* (genotype : *Juvavites bacchus* Mojsisovics, 1893) but this also can now be claimed as a distinct genus, since its relation to *Jovites* rests merely on Smith's assertion, whereas others may prefer to accept Mojsisovics's interpretation of *B. bacchus* as a globose Juvavitid. Moreover, Smith's own *Jovites pacificus* is not really typical and not much like *J. spectabilis* Diener (e.g. B.M., No. C. 28653), with which he compared it, or *J. mercedis* Mojsisovics, from Hallstatt, *J. daciformis* Diener, from Byans and the var. *timorensis* Welter. The inner whorls of the latter, however, do resemble *Bacchites*.

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[1] Arthaber (1911) attributed the family to Diener.

Halorites itself is represented in the Collection by examples from the Hallstatt area, including a number of specimens of the typical species, *H. ramsaueri* ; there are also examples from India[1] and Timor, including *H. macer*, *H. sundaicus*, and other species described by Welter. Many of the Timor Halcritids are not yet named individually ; most of them seem to be *Juvavites* and *Anatomites*.[2]

The second genus above mentioned (*Juvavites*), in Mojsisovics's original (1893) classification, included the two subgenera *Anatomites* (genotype : *Juvavites rotundus* Mojsisovics, 1893) and *Dimorphites* (genotype : *Juvavites selectus* Mojsisovics, 1893). Both *Anatomites*, which comprises many species, and *Dimorphites* have since been accepted as distinct genera, as has *Griesbachites* Mojsisovics (genotype : *G. medleyanus* Stoliczka sp., 1865) which was added as an independent genus to *Juvavites* by its author in 1896(*a*). The latter genus, as restricted by Mojsisovics in 1893, included only the group of the "*continui*," with straight or only slightly flexuous ribs running uninterruptedly across the widely arched venter. The group of the "*interrupti*" which, however, were also left in *Juvavites*, have the costation broken along the siphonal line, since the ribs on the two sides are not opposite. *Anatomites* has a similar ventral aspect, but constrictions with paulostome ribs which may cut off, obliquely, a number of ribs behind them. The final body-chamber, again, may be smooth.

Griesbachites, as already mentioned, was also established for certain *Juvavites* (and *Anatomites*), and after being emended by Diener (1908*a*), Welter (1914) and Diener again (1920*c*), is now used for those forms of *Juvavites*, without constrictions, in which marginal nodes or clavi are developed already on the septate part. In one Timor example of *Griesbachites* (No. C. 40617) these marginal nodes are extremely irregular.

The somewhat similar "*Anatomites*" with marginal nodes also developed already on the chambered whorls, but with constrictions, were separated by Welter (1914) as *Molen-*

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[1] Including the forms described in Crick's paper on *Amm. robustus* Blanford, from the Himalayas (1903) and a few duplicates in the Geological Society Collection.

[2] The Malayan ammonite labelled "Species A," in Newton (1925) is an impression of a *Juvavites* (or *Anatomites* ?), but has no distinct constriction. It is difficult to know why Newton did not figure the better half of the impression, instead of the poor counterpart (No. C. 25768).

graaffites (genotype : *M. hanni* Mojsisovics sp., 1896*a*). One fine Timor example of this genus has a diameter of 160 mm.

Two other genera closely allied to *Juvavites* are *Gonionotites* Gemmellaro, 1904 (genotype : *G. italicus* Gemmellaro, 1904) and *Indojuvavites* Diener, 1916*e* (genotype : *Juvavites angulatus* Diener, 1908*a*). One of the chief characteristics of *Gonionotites* is its change of shape and ornamentation in more advanced stages. The outer whorls lose the *Juvavites* or *Anatomites* ribbing and retain only slight marginal costation, sometimes associated with marginal nodes, until finally they become quite smooth. In *Indojuvavites* the early *Juvavites* or *Anatomites* stage is apparently confined to a very small diameter, while later there is more resemblance to *Dimorphites*, with close, falciform ribbing. The ribs meet on the periphery in sharp Vs, pointing forwards, and in both the compressed and more inflated varieties the ventro-lateral shoulders are well rounded, not angular, as in *Dimorphites*. The Museum possesses two of Diener's original examples of *I. angulatus* from West of Lilang, Spiti, and a good selection of *Gonionotites* and *Dimorphites* from Sicily, the former also from Timor.

The genus *Parajuvavites*[1] Mojsisovics, 1896*a* (genotype : *P. blanfordi* Mojsisovics, 1896), created for twelve species from the Norian Bambanag Limestone, differs from *Juvavites* only in its excentrumbilication ; but the genus *Heinrichites* Diener, 1920 (genotype : *H. paulckei* Diener, 1920*c*), introduced as a sub-genus of *Gonionotites*, is now also kept distinct. The inner whorls in both genera resemble *Juvavites* or *Anatomites*, but later they become flatter. *Gonionotites*, indeed, before the final body-chamber becomes inflated again, might be mistaken for a member of some smooth discoidal stock, whereas *Heinrichites* develops fine spiral ornamentation, recalling that of *Sagenites*. It may, however, show considerable resemblance to *Malayites*, mentioned below, but this retains the Juvavitid characters to a greater extent. On the other hand, the young of *Heinrichites* may look much like *Indojuvavites*, though they are rather different from *Dimorphites*, another related genus with more discoidal aspect than most Haloritids, but with an angular periphery. *Hein-*

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[1] This genus is represented by an example of *Parajuvavites feistmanteli* (Griesbach) from the *Halorites* beds of Bambanag Cliff (No. C.28651) and by *P.* cf. *jacquini* Mojsisovics, from the *Tropites* Limestone of Byans (C.28650).

richites paulckei is common enough to have been chosen as the characteristic fossil of the lowest Norian.

The genus *Gümbelites* Mojsisovics, 1896*a*[1] (genotype: *Heraclites* (*G.*) *jandianus* Mojsisovics, 1896*a*) was first established as a sub-genus of *Heraclites*, possibly on the strength of the short body-chamber. The smooth, ventral zone is rather unusual, but the dolichophyllic suture-line apparently agrees with that of the Haloritids; and, as Diener (1913) has shown, the affinities of *Gümbelites* are not with the widely different genus *Heraclites*, but rather with the group of *Juvavites interruptus*. *Gümbelites* is much rarer than the other Haloritids here cited, but it has also been found in Timor, whence have been recorded the following three genera.

The genotype of the first, *Amarassites* Welter, 1914 (genotype: *A. egrediens* Welter, 1914), was considered by Diener (1923) to be identical with *Amm. semiplicatus* Hauer (1850). As this species was included in *Halorites* by Mojsisovics, *Amarassites* must be a close ally, although it is said to be less nearly related than the genera *Jovites* or *Homerites*. It has a more discoidal shape on the whole, and a relatively open umbilicus, an excentrumbilicate outer whorl, and a fastigate periphery. The only Timor example in the Collection so far named (No. C. 40616) is slightly worn, but the suture-line is well displayed.

The genus *Malayites* Welter, 1914 (genotype: *M. informis* Welter, 1914) represents another Juvavitid with spiral ornamentation, like *Sagenites* or *Heinrichites*. A fine example of *M. singularis* Welter, from Nifoekoko, Timor (No. C. 40614), still septate at 100 mm. diameter and showing the suture-line well, has the usual black manganese oxyde-coating on the pale flesh-coloured marble matrix and the delicate spiral lineation was not noticed for a long time. The genus includes two species described by Welter as *Sturia*, but there are true *Sturia* from Timor in the Collection, probably *S. mongolica* (see *Psilosturia*, p. 153), with only peripheral spiral striation, one example being 155 mm. in diameter (No. C. 40615).

A special Timor element is the genus *Indonesites* Welter 1914, based on the very variable species, *I. dieneri* Welter 1914. The forms included in this species have been referred to *Anatomites*, *Bacchites* ?, and *Jovites*, and the suture-line is of the type of that of *Bacchites bacchus*, but the faint keel is

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[1] The spelling '*Guembelites*' is contrary to the rules.

reminiscent of *Jovites*. The contracting mouth-border and the keel are against inclusion in *Juvavites*. The Collection includes the globose " form 1 " (No. C. 21789) and the more slender " form 2 " (No. C. 21790), and the degenerate suture-line is the most striking character of the otherwise almost featureless shells.

The genus *Waldthausenites* Welter, 1914 (genotype: *W. malayicus* Welter, 1914), already mentioned under Tropitidae, is now included in the present family, if with some doubt. The ribs meet at an angle on the periphery which causes a peculiar keel to form, as in some Quenstedtocerates of the Jurassic, but quite unlike anything found in the Haloritidae. Welter even compared *Waldthausenites* to the widely different genus *Sirenites*, with the lateral tuberculation replaced by spiral striation, as in *Malayites*, but the degenerate suture-line alone indicates more affinity with Haloritids. Diener had it in Tropitidae on account of a distant resemblance to *Discotropites;* but the periphery suggests a Haloritid origin (as the comparable *Cadoceras–Quenstedtoceras* derivatives of Macrocephalitids acquired a crenulate periphery).

The genus *Miltites* Mojsisovics, 1893 (genotype: *M. rastli* Mojsisovics, 1893, *fide* Diener, 1915*a*) is now also included in Haloritidae, following Hyatt (1900) and J. P. Smith (1927*a*). It is a dwarfed, reversionary type in the latter's interpretation, but it must be admitted that Welter's " *Sibirites* " *miltitiformis* (1914) is transitional to the Metasibiritidae, discussed above. Mojsisovics, it will be remembered, included *Miltites* in his sub-family Sibiritinae (of the Tropitidae). On the other hand, contrary to J. P. Smith, I would include the genus *Barrandeites* Mojsisovics, 1893 (genotype: *B. turbina* Dittmar sp., 1866), not in Tropitidae, but in Haloritidae, following Mojsisovics and Arthaber (1911). If *B. dittmari* Gemmellaro (1904) is really close to the typical *B. turbina*, the prominent *Tropites*-keel is rather against this classification and the periphery is, of course, entirely different from that of the genus *Girthiceras* Diener, 1909*a* (genotype: *G. pernodosum* Diener, 1909*a*), which is included here only with doubt. As its author pointed out, the suture-line of *Girthiceras* is dolichophyllic, resembling that of *Halorites* and *Juvavites*,[1]

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[1] The use of " Haloritinae " in this connection (really a sub-family name), is probably due to faulty translation. The division of Haloritidae into two sub-families, Haloritinae and Juvavitinae, was at one time considered desirable, but abandoned on account of the many practical difficulties.

and there is a certain similarity to *Miltites ;* but the flattened venter is an unusual feature.

Still less definitely attributable to Haloritidae is the genus *Leconteiceras* J. P. Smith, 1914 (= *Leconteia* Hyatt & Smith, 1905, pre-occupied) established for *L. californicum* (Hyatt & Smith, 1905). In spite of its resemblance to " *Polycyclus* " (*Hannaoceras*), mentioned on p. 85, and of its " *Sagenites*-like inner whorls,"[1] this form, represented by a considerable number of specimens, is said to be a " reversionary " Haloritid by Smith in his latest work (1927*a*).

The structure of the test of *Leconteiceras* in thin section is interesting. It begins to thicken rapidly, after the first whorl and a half, and at 2½ whorls (diameter just over 2 mm.) it appears to split in two, forming a thick outer layer and a thin inner. Then depressions, shallow at first, appear on the thick outer test, but they soon deepen, and at 3½ whorls (or 4·5 mm. diameter) they penetrate the double test to about half its thickness (which itself is about a fifth of the diameter of the whole whorl). There may be an abrupt cessation of these deep and narrow furrows which are covered on the outside by a level third or outermost layer, but since this phase in which the test is merely wrinkly (Voorthuysen, 1940, fig. 55, p. 126), lasts only for a short distance, it is probably due to some abnormality. The intercostal furrows (or flask-shaped hollows, in section) soon reappear and deepen still more until the thick outer or, rather, second layer, at the bottom of the hollow touches the thin inner or first layer. There are about ten or eleven of these hollows to the half-whorl at 7 mm. diameter, but after that the test is not preserved.

The very thick siphuncle is not yet external at 12 mm. diameter, and a whorl earlier it is well below the double test. At a whorl-height of 2 mm. the siphuncle and double (or treble) test occupy half the total. In the example figured in Smith's (1927*a*) pl. xxix, figs. 14–16, the siphuncle appears to have been external at well under 9 mm. diameter.

The fact that the intercostal spaces, narrow on the surface, widen out below, in what must have been a thick but hollow shell, was rather unsuspected. There is no trace of the " Glyphioceran " constrictions of the original description which were said to cease at 4 mm., and presumably would show

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[1] This does not apply to thin sections, *Sagenites* being quickly coiled (about 3½ whorls at 12 mm. diameter), whereas *Leconteiceras* is polygyral (5½ whorls at the same diameter).

(in section) between the initial constriction and the appearance of the ribs. But they are not visible on the two larval examples figured in pl. xxix, figs. 17–21; and I cannot see any resemblance between the costal bulges of these figures and the tuberculate umbilical edge of the Carboniferous *Gastrioceras*.

The genus *Pseudohalorites* Yabe 1920, (genotype: *P. subglobosus* Yabe, figured in 1920 and described in 1928), may have nothing to do with the present family, for it has even been doubtfully referred to the Permian and may be of Lower Triassic age (Kutassy, 1933). The suture-line is against comparison with *Halorites* and *Juvavites*, and the absence of a median saddle in an external lobe that is serrated, seems suspiciously unreal.

An entire external lobe, however, is found in the genus *Paraganides* Hyatt & Smith, 1905 (genotype: *P. californicus* Hyatt & Smith, 1905), which is now included in the family Haloritidae, partly because, from the evidence of the siphuncle in median section (p. 163), it seems to be a member of the Tropitida. Its sub-globose shape suggested reference to the Nannitinae to Hyatt & Smith (1905), and later (Smith, 1927*a*), to the Ptychitidae, but, as shown below, this family is not likely to have produced a form with the internal features of a Tropitid. The undivided external lobe of *Paraganides* is taken to represent merely a further simplification of the *Anatomites* suture-line.

The degenerate Haloritid *Tardeceras* Hyatt & Smith, 1905 (genotype: *T. parvum* Hyatt & Smith, 1905) has to be added here, as already mentioned under the family Metasibiritidae (p. 104). It is clear that Smith misinterpreted the genus *Metasibirites*, so that *Tardeceras* has to be reinstated. It is well represented in the Collection, from Brock Mtn., Shasta Co., California, which fauna, however, includes only various *Anatomites* as other members of the Haloritidae, in addition to *Leconteiceras*, *Sagenites* and, of course, a very large number of other ammonites.

Six young specimens of *Tardeceras* (of the type of *T. parvum*) were sectioned, but only one section is central enough to show the very small protoconch and all the septa, from the start. Even this slide, however, does not show the siphuncle or its funnels until the third whorl. These funnels are seen in all the six sections and they are not quite ventral even on the last septum before the end of the camerate stage, between diameters of 7·25 and 10 mm. The last eleven septa are approximate in one specimen, but those of the earlier half of the same whorl are broken and could not be counted. The three next inner whorls have 12 septa each. Another example has 16 septa on the last septate whorl ; a third has 12, fairly regularly spaced and without approximation. One specimen shows a constriction, about a whorl from the end of the septate stage ; in another the inner whorls are elliptical and there is a scaphitoid kink with a very deep constriction at just over 2 mm. diameter. The thickness of the siphuncle in the third whorl (or at 2·5 mm. diameter) is ·25 mm., or about 25 per cent of the whorl-height. The test is getting very thick in the third and fourth whorls, and is half the thickness of the siphuncle at the end of the septate stage, but it is quite thin again on the outer whorl or the body-chamber, so far as can be seen. The small protoconch and the thick siphuncle are Tropitid characters, but the subventran position of the siphuncle is reminiscent of *Lobites*.

a. Sub-family SAGENITINAE, nov.

The genus *Sagenites* Mojsisovics (1879*a*) has for genotype : *S. reticulatus* Hauer sp. (1850), selected by Hyatt & Smith (1905), but Diener, in his ' Catalogue ' (1915), listed *Ammonites inermis* Hauer (1855*a*) as genotype. The former species, of the division *reticulati*, was the first species mentioned by Mojsisovics in 1879(*a*) ; the second, of the group *inermes*, was the first species described by Mojsisovics in 1893.

Sagenites has long stood apart from the more typical Haloritids on account of its ornamentation as well as its extremely subdivided suture-line, reminiscent of that of the Lower Liassic *Liparoceras* (*Becheiceras*) of similar whorl-shape. Mojsisovics's two divisions of *inermes* and *reticulati* have not so far been separated as generically different, though *S. biplex*, for example, has even been considered (Diener, 1920*c*) to be a species of *Malayites* rather than a true *Sagenites*.

Trachysagenites Mojsisovics, 1893 (genotype : *Ammonites erinaceus* Dittmar, 1866) was established, as a sub-genus, for Mojsisovics's third division of " *spinosi*," but itself includes now a considerable number of species. It is therefore separated as a distinct genus and, with *Sagenites*, is included in a sub-family Sagenitinae. This will reduce the overcrowded family Haloritidae and allow for the origin of *Sagenites* as a stock, independent of *Halorites* and *Juvavites*, as suggested already by Mojsisovics and again by J. P. Smith (1927*a*). I do not accept the origin of these three stocks in *Acrochordiceras* (see Part IV, p. 393), a highly specialized Ceratitid development of the Middle Trias ; and I would look for the ancestor of Sagenitinae as of Haloritidae, in a smooth stock that also gave rise to Episculitinae.

After having considered them Haloritids for many years, Diener (1925) suddenly transferred *Sagenites* and *Trachysagenites* to the family Ptychitidae. There is no clue to this change of opinion in his descriptions of these genera in 1920(*c*), but in Diener's diagnosis of the typical *S. inermis* in 1925 it is pointed out that the external lobe is very short, as in the *rugiferi* group of *Ptychites*. *Sagenites* is of Carnian to Norian age, and might possibly be a specialized derivative of the Anisian-Ladinian Ptychitidae, which is one more reason for separating it from the typical Haloritidae. But I may say that the suture-line of the young of *Trachysagenites herbichi* (Mojsisovics), figured by Hyatt & Smith (1905), does not support Diener's latest view. Even the suture-line of the Californian *Alloptychites meeki* (Hyatt & Smith, see p. 151) has a much wider external lobe and more numerous elements.

Apart from some Alpine and Timor examples of *Sagenites* and *Trachysagenites*, the Collection includes a number of specimens of the Californian type of *T. herbichi* and presumably of *T. smithii* Diener. A section of the nucleus of one of these Californian *Trachysagenites* (all septate at 18 mm. diameter) was unsatisfactory owing to the coarsely crystalline matrix. It showed a fairly wide, external siphuncle near the end. The increase in whorl-height, i.e. in the spiral, is relatively fast, as in Haloritidae in general, but the convex septa resemble those of the slowly increasing types, which may be correlated with the globosity. There is one conspicuous constriction at about 5 mm. diameter.

b. Sub-family EPISCULITINAE, nov.

The three groups now referred to this sub-family are believed to be Haloritids in the wider sense, showing not only simplification of the suture-line, but uncoiling of the body-chamber, so that they were all at one time included in the genus *Isculites* Mojsisovics. As explained below (p. 155), this Middle Triassic genus was given a new name in error by Diener

(1916*e*), who thus wrongly restricted *Isculites* to a group of Norian forms with *Amm. decrescens* Hauer as the genotype. A mere exchange of names being prohibited by the Rules, it becomes necessary to rename the Norian so-called *Isculites*, grouping themselves around *Amm. decrescens* Hauer (1855*a*, p. 159, pl. v, figs. 6–7) and **Episculites**, nom. nov., is here suggested, the type being Hauer's original, refigured in Mojsisovics (1893, p. 65, pl. lxxxvii, fig. 3). *Amm. obolinus* Dittmar, already referred to in connection with *Tornquistites* (p. 96), may be connected with the type, but it is not so clearly a Haloritid; it is compressed, unconstricted, and there is only slight excentrumbilication.

These typical forms with 'entire' suture-lines may be connected with similar ammonites having ammonitic septal edges, for which another name becomes necessary. They are now referred to **Euisculites**, gen. nov., created for *Isculites bittneri* Gemmellaro (1904, p. 250, pl. xv, figs. 8-12), which genus probably includes all the other species of "*Isculites*" described from Sicily as well as forms like "*I.*" *heimi* Mojsisovics. This Carnian species, or at least the Indian example figured by Diener (1906*a*, pl. xv, figs. 1*a*–*c*), happens to resemble the true *Isculites hauerinus* in having a sub-ammonitic suture-line and a peculiar, parallel-sided external lobe. There are differences, however, especially in the auxiliaries, though these are, perhaps, not of much importance, in view of the variability in this respect, among the Sicilian species, possibly due to variations in thickness or whorl-shape. The Anisian forms, however, are here believed to be derivatives of the Ptychitid root-stock, so that the resemblance to more or less homoeomorphous Haloritid developments is accidental. In the Timor "*Isculites*" *eunapii* Diener (1923), described as a larger edition of the European *Amm. decrescens*, the affinity with Haloritids is unmistakable, though the suture-line is unknown and it could be either an *Episculites* or an *Euisculites*.

The presumably allied "*Isculites*" *dieneri* Pakuckas (1928), with two ventral rows of tubercles, has a curious resemblance to *Daphnites berchtae* Mojsisovics. Combined with its extremely simple suture-line, the contraction of the body-chamber of this Timor species was said to point to affinity with *Episculites*, but this may, perhaps, be over-rating the value of excentrumbilication as a basis of classification. The suture-line was described as having very faintly serrated lobes and as resembling that of *E. subdecrescens* (Mojsisovics). Yet the two ventral rows of nodes and the umbilical bulges or tubercles give this form a peculiar aspect, just as *Gümbelites*, of which it may be a development, is distinguished from all other Haloritids. The new name, **Hypisculites**, gen. nov., is therefore now proposed for it, the genotype to be "*Isculites*" *dieneri* Pakuckas (1928, p. 171, pl. i, figs. 3*a*–*c*).

F. Family DIDYMITIDAE Haug, 1894.

The name Didymitinae seems to have been first used by Haug (as a sub-family of Arcestidae) in 1894, and it was raised to family rank by Mojsisovics in 1896(*a*). The family was discussed again in the Supplement to Mojsisovics's great Hallstatt work in 1902(*a*), so that the claim of Arabu (1932), to the family Didymitidae as a "new group" (in which he included *Isculites*), seems somewhat belated. Haug had pointed out that unlike the other members of the Arcestidae (i.e. Arcestinae, Joannitinae and Lobitinae), the genus *Didymites* was characterized by what he called a stenophyllic suture-line; and he suggested that *Didymites* might, perhaps, be allied to certain Tropitidae. Mojsisovics then definitely transferred the family from the Leiostraca to the Trachyostraca (super-family Tropitoidea) on the basis of the simple suture-line, with the number of lobes below the normal; and he thought that *Didymites* might have developed from the Haloritidae by the gradual loss of the transverse ribbing. That is to say, certain faintly ornamented Juvavitids like *Bacchites* might be held to be related to the ancestors of *Didymites*. On the examination of large examples of this genus (e.g. *D. subglobus* among the many examples of *Didymites* from Mojsisovics's own collection and some distinctly keeled Timor specimens in the Museum) the faint Haloritid ornament and occasional slight keel on the body-chamber are indeed striking. Arthaber's (1927) contention that the acquisition of such ornamentation only in old age was an indication of a progressive, not a retrogressive, stock, cannot now be accepted by the writer, who has doubted the value of recapitulatorial "evidence" on so many occasions. Moreover, the young of *D. globus* (Quenstedt) show not only ornament and spiral lines, but even the constrictions of Haloritidae.[1]

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[1] One example of *Didymites* cf. *tectus* Mojsisovics, from the *Tropites* Limestone of Byans (B.M., No. C. 28665), has a ventral sulcus, but this is not in the median line, and therefore presumably due to some injury.

Arthaber's reference to "*Sirenites*" (p. 121) is no doubt due to a slip, but he was right in stating that in the Timor fauna *Tropites malayicus* Welter was very close to *Didymites*.

In a first provisional sorting of the Timor material acquired by the Museum in 1930, I was struck by this unexpected resemblance and considered it as confirmation of the removal of *Didymites* from the Leiostraca. It made it all the more difficult to understand Diener's change of view in 1925. After having followed Mojsisovics for many years, at least down to 1920 (*c*, p. 515), Diener, in his part (IV) of 'Leitfossilien,' not only transferred the family Didymitidae back to the Leiostraca, i.e. the Arcestida,[1] but declared it to contain only the single genus *Didymites* Mojsisovics, 1875 (genotype: *Ammonites globus* Quenstedt, 1849). Yet Diener himself, nine years before, had created two more genera, namely *Paradidymites* Diener, 1916*e* (genotype: *D.* nov. sp. ind., Lukas Waagen, 1899 p. 550, figs. 2*a-c*, p. 551. = *P.* **waageni** nom. nov.) and *Timorodidymites* Diener, 1916*e* (genotype: *D. malayanus* Welter, 1914), both of which are now accepted as valid, and not only as sub-genera.

The more or less globose shape of the forms of *Didymites*, it is true, makes them look externally like Arcestids, with the final whorl becoming excentrumbilicate, sometimes very markedly (*Didymites* nov. sp. ind., Diener, 1920*c*). Hyatt (1900) thus included the family Didymitidae Mojsisovics in the Arcestida, despite its author's correction, while in J. P. Smith's badly "revised" second edition of Zittel's 'Text-Book' (1913) *Didymites* was even reduced to a mere genus in a sub-family Arcestinae. The comparable treatment, if less assured, in Broili's revision of the 'Grundzüge' (1924) has already been criticized by Arthaber.

J. H. van Voorthuysen's (1940) beautiful researches on the Timor *Didymites* tend to confirm its relationship to the Tropitida, and show that the internal structure differs from that of *Arcestes*, in which the siphuncle is nearly external from the start. *Didymites*, on the other hand, has a siphuncle that remains away from the venter until the end, even more so than in *Lobites*. The position of the siphuncle was verified in sections of two Hallstatt *Didymites* from the Mojsisovics

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[1] Diener explained his change of view in 1923 (footnote to p. 266), when he believed that *Didymites* might be closer to the Lobitidae than to the Haloritidae on the supposition that the divided lobes in *Lobites* were analogous to the divided saddles in *Didymites*.

collection (Nos. C. 5715*a*, *b*) labelled *D. globus* (Quenstedt). One of the sections is transverse and shows the deep and narrow umbilicus of Quenstedt's pl. xviii, fig. 14*d* (*Amm. gaytani*) but the whorls are still more depressed, so that at 15 mm. diameter the thickness is the same, or 100 per cent., while at 8·5 mm. the thickness is 10·25 mm., or 125 per cent. of the diameter. In the longitudinal section, the siphonal funnels are seen to the last septum at 21 mm. diameter, and their position is centroventran to propioventran (Hyatt). There are only six whorls present, however, even then, so that the reconstruction, in v. Voorthuysen, shows probably at least one whorl too many. The number of septa per whorl is 24, 16, 10, 10, 10, counting inwards, but only a few septa of the innermost whorl are seen, as the section is not quite central. The funnels are longer than in the Timor *D. subglobus* Mojsisovics, especially the outer (ventral) portion, even on the last septum.

Considering that the siphuncle at the last septum can be still subventran or propioventran in such unrelated forms as the Clionitid *Traskites fairbanksi* (Hyatt & Smith) or the keeled *Neodalmatites parvus* (Smith), I am retaining *Didymites* in the Tropitida, not on the evidence of the thin sections, but on the obvious resemblance in the adult and the evidence of the suture-line. The family Didymitidae is thus taken to be one of the families of the Tropitida, as Mojsisovics held in 1902(*a*), and Diener still in 1920(*c*).

VIII. Super-family LOBITIDA Hyatt, 1900.

A. Family LOBITIDAE Mojsisovics, 1893.

This family was first established as a sub-family, then raised to a full family in 1896(*a*), and in 1900 Hyatt made it a super-family of the same standing as the Arcestida. This classification is here adopted for reasons which will appear in the sequel. The development of the suture-line of *Lobites*, traced by Branco (1879), is very unusual, and Hyatt rightly directed attention to it. Yet in connecting Lobitida with the entirely different Palaeozoic Prolecanitida, Hyatt was influenced only by the appearance of the suture-line in the adult.

With its simple, lanceolate lobes and saddles, the suture-line of *Lobites* is indeed very different from that of any other Triassic ammonite and much like that of some Palaeozoic goniatites, for example, certain forms of *Agathiceras*, even in the number of elements. Arthaber (1927) thus also linked *Lobites* with the Carboniferous-Permian family Agathiceratidae (*Agathiceras* having been left in Prolecanitidae by Hyatt in 1900). In spite of what Arthaber termed the Palaeozoic type of suture-line of *Lobites*, there is really little external resemblance between this Upper Triassic genus and the spirally striate *Agathiceras*. Moreover, there is nothing in the Lower Triassic that would connect the two stocks, either morphologically or in the adult suture-line. Yet there is some distant resemblance between *Lobites* and *Agathiceras*, for now we know that the suture-line in the latter also resulted from the subdivision of an original lateral lobe (in *Proshumardites*), only this was trifid, not bifid, as in *Lobites*. Such bifid lobes are common in *Lytoceras* (here resulting from an original trifid lobe), and they produced a prominent median leaflet which, however, never attained the size of a full saddle, so far as is known. On the other hand, in the Arcestids the formation of new lobes and saddles proceeded from the umbilical lobe, inwards and outwards, so that Arthaber was right in objecting to *Lobites* being considered an abnormal offshoot of *Arcestes*, in Mojsisovics's meaning.

This connection, direct or indirect, of *Lobites* with the Arcestids is still generally accepted. In the second English edition of Zittel's ' Text-Book ' Hyatt's super-family was promptly abolished and *Lobites* reduced to a mere genus, doubtfully included in another Permian sub-family, Popanoceratinae, but it was again referred to the super-family of Arcestida. In Broili's 1924 edition of Zittel's ' Grundzüge,' *Lobites*, also with a query, was included in the equally Permian Cyclolobidae, presumable ancestors of the Arcestids. Diener (1925) cited the Lobitidae (again presumably as one of the Arcestids in the wider sense) after the Didymitidae which he thought formed a counterpart (suturally) to the former, their saddles being divided by deep lobes instead of the lobes being subdivided by saddles, as in the Lobitidae. It has already been mentioned (p. 116) that Diener's change of opinion was surprising, after having considered *Didymites* to belong to the Tropitida for so many years. Nevertheless, it is clear that *Lobites* also has only two lobes in its original suture-line, between the external lobe and the umbilical suture. This is the fundamental factor in considering the taxonomic position of the family.

Comparing the suture-line of *Lobites* (*Paralobites*) at 3 mm. with that of *Megaphyllites* at 2·5 mm. (in Branco), it is easy to see how the extra saddles arose, caenogenetically, from the median protuberances in the two lateral lobes ; and in the submegaphyllic *Indolobites* the similarity is still closer. Obviously, this is not recapitulation of the suture-line of a multilobate ancestor, and it is sufficiently remarkable to secure for *Lobites* a place of its own among the Triassic Ammonoidea.

It must not be assumed, of course, that the development of the suture-line is constant in a given genus or even species, or that it can always override the evidence of all the other characters, for example, those subtle morphological family characteristics that often indicate the probable relationship of a certain group. Even these, however, have misled observers ; and palaeontological literature abounds with types that were carried as ballast until some chance discovery (of perhaps an absolutely isochronous fauna) supplied intermediate forms and thus the key to their interpretation. In the development of the suture-line there are curious anomalies. For example, if the median saddle in the external lobe of *Arcestes maximiliani-leuchtenbergensis* (Klipstein) is high at 1·75 mm., and again at 4 mm. (Branco's figs. 1*o* and 1*q*, pl. vii, 1879), then it should not be low at 2 mm. diameter (*ibid.*, fig. 1*p*). Likewise, if *Paralobites nautilinus* (Münster), already cited, has three dorsal saddles at 3 mm. diameter, then the number should not be reduced to 2 at 5 mm. But apart from such discrepancies, the species of *Arcestes*, above cited, shows lateral lobes that gradually become trifid. Yet in the same species (now named *A*. (*Proarcestes*) *bicarinatus* Münster sp.) Schindewolf figured a suture-line which has two fully formed bifid saddles at only 1 mm. diameter—one more than is shown by *Paralobites* at 1·5 mm. I am fully aware of the difficulty of identifying the small ammonites of the St. Cassian fauna, as my criticisms of many species in the Klipstein Collection will show ; and it is not impossible that the forms figured by both Branco and Schindewolf have been misidentified specifically, if such small ammonites allow of specific determination at all. The point I wish to emphasize, however, is that these figures, as those of the allied *Megaphyllites*, *Sphingites* and others, have to be interpreted as broadly as the varying features of the early whorls displayed in thin sections.

The evidence of the numerically under-developed lobes in the suture-line of young *Lobites* is not the only objection to the grouping of this genus with the Arcestida. There are also the strong radial ornamentation and the excentrumbilication of the body-chamber, with resemblance to that of the Isculitidae or of certain Haloritidae (Pompeckj, 1894). This is shown, for example, in such large constricted forms as the Anatolian *Lobites philippii* Mojsisovics, as figured by Arthaber (1914), and as represented in the Collection by a number of specimens, one of which was sectioned. This species has not only strong Haloritid ribbing, but the second saddle of its suture-line exceeds in height both the external and the first lateral saddles on either side. Since this largest saddle has almost certainly resulted from the small protuberance in the lateral lobe, as in *Paralobites*, the common assumption that the lateral saddle is recognizable by its size is clearly erroneous.

It remains to be seen whether the transfer of *Lobites* to the Trachyostraca, or at least its removal from the Arcestida, is justified by the structure of the siphuncle in the median sections. The siphuncle in *Lobites* is fairly thick in comparison with the diameter of the narrow whorls ; in *Arcestes* it is thin. It is also subventran in *Lobites*, that is, not quite external even at the end of the septate stage ; in *Arcestes* it is nearly external from the start. In the small *Paralobites pisum* (Münster) from St. Cassian, the body-chamber (1½ whorls when complete) often begins at only 5 mm. diameter. In two out of nine sections the siphonal funnel could be seen on the last septum, but in four others only at the second, third, or fifth septum from the end, always away from the outer margin.

In all the sections the centre had been replaced by crystalline calcite, and only two retained the outline of the innermost whorls, with only one showing all the septa. Most sections, however, retained siphonal funnels, here and there, from the third whorl onwards, and they were already then near the outer margin, as in Branco's fig. ii*d* (pl. vii). The number of septa varies ; it may be 12 per whorl, but in the best section there are 10 in the first whorl, followed by 9, 9, and 8 in the suceeding 3 whorls, and by 7 in the final half-whorl, the last 3 septa being closer than the rest. The end of the 4½ whorls of air-chambers in this section is at 6·75 mm. diameter.[1]

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[1] These sections of *Paralobites pisum* seemed curiously reminiscent of some sections of the equally small *Agathiceras suessi* Gemmellaro I prepared many years ago. On re-examining them I remembered the similar mode of preservation, with the inner whorls replaced by crystal-

An example of *Lobites philippii* Mojsisovics, from the Lower Carnian of Tepeköi, Gulf of Ismid, Asia Minor (No. C. 13991), of a diameter of 45 mm. and with 1½ whorls of body-chamber, has the siphuncle not quite external even at the end of the septate part, at 22 mm. diameter. The siphuncle then occupies about a quarter of the diameter of the whorl and a volution and a half earlier, almost a third, but the innermost whorls are again crystalline. The last 3 septa are closely spaced and the next 7 slightly so, but on the succeeding inner whorls they are very widely spaced, there being only 7 per whorl, counting inwards, until they disappear towards the centre.

In *Lobites* the greatest diameter of the protoconch is about ·35 mm., as against only ·25–·3 in the Tropitida, or ·55 in *Ptychites*, ·5 in *Arcestes* and *Joannites*, or ·6 mm. in a Timor example of the last genus (see p. 133). In spite of this, the sections of *Lobites* are not very different from the section of *Joannites* figured by van Voorthuysen (1940, p. 103, fig. 43). In this the siphuncle in the third whorl has a thickness of about 25 per cent. of the narrow whorl, yet its real width is only ·1 mm., or only half of what it is in *Ptychites*. Since it takes up about 40 per cent. of the diameter of the third whorl in that genus, it appears to be more massive even than that of *Tropites*.

All this is somewhat inconclusive ; and, in view of the vagaries of the siphuncle in other genera, it seems scarcely sufficient to warrant the removal of the Lobitida from the Leiostraca, or their inclusion, as a family, in the Tropitida. They would certainly seem out of place to many in that superfamily. It may be years before the development of the *Lobites*-like "genus" *Ptycharcestes* (see p. 128), or of the rarer Lobitids like *Orestites* or *Indolobites*, can be studied ; meanwhile, however, there is nothing more than general resemblance in characters, like the closing of the umbilicus by a callosity to link Lobitids with the Arcestida. The

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line calcite, and I was struck by the regularity of the septation. No fewer than 12 out of 17 slides had 16 regularly spaced septa on the last chambered whorl, which varied from 4 to 13 mm. in diameter. Three others had 15, 17 and 18 septa, but two were defective. There was no trace of approximation of the final septum in any section. The siphuncle with its long funnels was equally constant, at or near the venter on the last septate whorls, nearer the centre where seen on the earlier whorls (one of these sections is referred to in Böhmers, 1936, p. 70).

frequent appearance of constrictions in *Lobites* also cannot be relied on in attaching it to the Arcestids rather than the Ptychitids or the Trachyostraca. The variation, shown in this respect by the young of *Gymnites* (see p. 173), should be a warning. In the best section of *Paralobites pisum* the first constriction is at about 360°, as in many other ammonites of no affinity whatever. The succeeding 2½ whorls have no constrictions at all, but then they reappear, at intervals of 180°, to the end of the septate stage. In other sections, however, there may be three constrictions, or labial ridges, to the whorl at diameters of 4 mm. and below, whereas in *Lobites philippii* there is only one constriction, on the third whorl, at a diameter of 3 mm. The initial constriction, in this, as in all the other eight sections of *Paralobites*, is invisible owing to the crystalline matrix.

In view of so much uncertainty, it seemed encouraging to find an almost exact parallel to the suture-line of the young *Paralobites* (at 1·5 mm. diameter) in the adult septal edge of *Thanamites*, here provisionally attached to the family Isculitidae. There is the same lateral lobe with its median protuberance ; both suture-lines have only one more lobe near the umbilical suture ; and there are the same rounded and entire saddles. Whorl-shape and involution in *Thanamites* also agree well enough with the same characters in *Lobites*. Diener, however, stated that the suture-line of *Thanamites* showed it to be a representative of the Trachyostraca, notwithstanding its external resemblance to Arcestoidea ; and he compared it to *Didymites*, which at that time he believed to be a Tropitid. On going into the question in more detail, it was soon found that there were as many difficulties in accepting *Thanamites* as a forerunner of *Lobites* as any Arcestid. Bifid lobes, in fact, are common, and they may or may not mean anything. The age is no obstacle, since both genera appear in the Ladinian. Kutassy (1933) cited *Lobites bouei* Mojsisovics, from the Anisian of Serbia, but by error, for Zivkovič (1931) correctly recorded this species as Ladinian. The other supposed Anisian Lobitid, namely, *Indolobites oldhamianus* (Stoliczka), is now admitted to be of doubtful age and is not a pre-Ladinian ancestor. Moreover, there are yet other new types of Lobitids in the Ladinian, some of which are not even named.

The isolated *Lobites* (?) *aberrans* Mojsisovics (1882) has been described as more excentrumbilicate than any other species of *Lobites*, but with involute, rounded inner whorls. The quadrate last whorl and the oblique constrictions are certainly quite unlike *Lobites*, but, unfortunately, the suture-line of that form is unknown. In the reputedly comparable *Arcestes evolutus* Mojsisovics (1873), of much later (Norian) age, the constrictions are rather different, and the slender and rounded last whorl also indicates that the resemblance is merely superficial. Renz (1911) thought that *Lobites* (?) *aberrans*, or at least the form he described from the Carnian of Greece, was probably closer to *Sphingites* than to *Lobites*, or perhaps referable, with *Arcestes evolutus*, to a special group of Arcestids; but it seems to me that neither of Mojsisovics's species belongs to *Sphingites*. Thus *Lobites* (?) *aberrans* may well turn out to represent a new type when its suture-line becomes known.

Another new and interesting Ladinian form of *Lobites* is *L*. nov. f. ind. Mojsisovics (1882, p. 179, pl. xxxix, fig. 12), which has remarkably broad and short saddles, different from those of any other known form of *Lobites*. If this unnamed species with flattened whorls resembles the root-stock of the family, then neither the globose, Arcestid whorl-shape nor the Prolecanitid lanceolate saddles of the typical forms can be looked upon as original features.

Unfortunately, it is not known whether the second saddle in this new form (called the first lateral saddle by Mojsisovics) results from the protuberance in the original principal lobe, as in other *Lobites*. This is probable, however, and in any case, so unusual that it can scarcely be compared with the mere presence of a bifid first lateral lobe in any other ammonite-stock. For example, such lobes occur in the young *Tropites*, as mentioned below (p. 159), or in *Paradidymites*. In this last genus, not only the principal lobe, but even the saddles are the exact opposite of what they are in the true *Didymites*, and yet the two genera agree in all other characters, so far as is known. The distinction between a bifid and a trifid lateral lobe was once thought to be of great importance as a means of dividing the Neocomian Crioceratids into descendants of *Lytoceras* and " *Hoplites* " respectively, but this also turned out to be a complete illusion (Spath, 1919, p. 220).

The genus *Didymites*, finally, agrees with *Lobites* in having a siphuncle that never becomes external, throughout the septate portion, although it is not so nearly external as in *Lobites*. In the Timor form of *Didymites*, figured by v. Voorthuysen (1940), the general appearance is that of *Lobites*, allowing for the variations in the number of septa, presence of constrictions, etc., previously referred to. In the Hallstatt specimens of *Didymites*, mentioned on p. 117, the resemblance to *Lobites* is equally pronounced, although there are no constrictions at all. But, in view of the difference in age between the Ladinian-Carnian *Lobites* and the Norian *Didymites*, the resemblance may be largely accidental, and Diener's latest views on the connection between the two genera were prompted partly by lack of more concrete evidence.

The genera included in this family, then, are: *Lobites* Mojsisovics, 1879*a* (genotype: *Clydonites ellipticus* Hauer, 1860) which occurs already in the Ladinian and perhaps even the Anisian; *Coroceras* Hyatt, 1877 (genotype: *Clydonites monilis* Laube, 1869), as emended by Mojsisovics (1902*a*), and retained for the *delphinocephalus*-group, with highly modified body-chamber; also the genus *Paralobites* Mojsisovics, 1903 (genotype: *Goniatites pisum* Münster, 1841), created for the smooth forms, with labial ridges. The genus *Psilolobites* Renz, 1911 (genotype: *L.* (*P.*) *argolicus* Renz, 1911) was originally introduced as a sub-genus for those smooth forms of *Lobites* which, at a diameter much larger than that of *Paralobites*, have neither constrictions nor ridges and pointed, not rounded, lobes. As in Arthaber (1927) and Johnston (1941),[1] *Psilolobites* is here taken to be a separate genus.

The genus *Indolobites* Renz, 1911 (genotype: *Clydonites oldhamianus* Stoliczka, 1865) includes a form of uncertain age which shows incipient subdivision of lobes (or saddles). It appears to owe its second saddle to exaggerated development of the protuberance in the original lateral lobe, as in *Paralobites*, and presumably all the other Lobitids, even the genus *Orestites* Renz, 1911 (genotype: *O. frechi* Renz, 1911) in spite of its author's reservations. This genus includes smooth forms that resemble Arcestids as well as Haloritids in whorl-shape, but the two halves of both the external and lateral lobes are trifid. Renz, while considering the "regressive modification" of the suture-line in *Indolobites* similar to that of *Orestites*, excluded the latter from the Lobitidae proper.

The genus *Lobites* is represented in the Collection by species from Hallstatt, Anatolia and the Peace River, British

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[1] In the description of a species of *Lobites* from Nevada, this author considered it necessary to add: "Soft parts of animal unknown."

Columbia (*L. paceanus* McLearn). The Klipstein Collection comprises twenty-seven specimens, of which fifteen are labelled in Klipstein's writing: *Belerophon* (sic) *nautilinus* Münster; three *Goniatites pisum* Münster; and two *Goniatites aequilobatus*, nob., including the figured example (pl. viii, fig. 14). The four constrictions in the last form are certainly striking; if not more oblique than drawn in Klipstein's figure, they are at least more tangential at the umbilical end, quite different from the two constrictions of Laube's fig. 2*c* of *L.* "*nautilinus*." According to Diener (1906*a*), "in the genus *Lobites* such a narrow circumscription of species had been introduced by Mojsisovics that a specific value was conceded to features which in other genera of ammonites could only be regarded as of varietal importance." Mojsisovics, it is true, gave a new name (*L. pisiformis*) to Klipstein's *L. aequilobatus*; but the two species, *L. nautilinus*, as figured by Mojsisovics in 1882, and *L. pisum* (= *Clydonites nautilinus* Laube, 1869, pl. vii, fig. 2), are well distinguishable among the material in the Klipstein Collection (21 examples of *Paralobites pisum* to 4 of *P. nautilinus*).

IX. Super-family ARCESTIDA Hyatt, 1900, emend.

When Neumayr (1875) divided the ammonites into four families, including the Arcestidae, he envisaged what we should now call super-families. Apart from some smaller adjustments, due to our much greater knowledge of the Triassic ammonites, his two families of Arcestidae and Tropitidae showed a remarkable approximation to our later classification of these ammonites into the two groups of Leiostraca and Trachyostraca; and, like Suess's grouping of the post-Triassic ammonites into *Lytoceras-Phylloceras*, on the one hand, and the rest on the other, it has always evoked my admiration. In the present super-family, the adjustments made to Hyatt's scheme are slight: (1) the Permian "forerunners" are now separated, because they were not necessarily the ancestors of the true Arcestidae; (2) the Didymitidae are excluded (see p. 115), although, as Hyatt correctly stated, the shell was globose as in Arcestidae, the striae of growth differed but slightly, and the differences in the suture-lines were not considered of fundamental importance by Arthaber even in 1927. Again, Hyatt's separation of the super-family

Lobitida for the one family Lobitidae and the one genus *Lobites* is now believed to have been justified, although hitherto the writer preferred to group the Lobitidae (Lobitinae in Mojsisovics, 1882) as a family within the Arcestida, whereas J. P. Smith, in his revised English edition of Zittel's ' Text-Book ' (1913), discarded both Lobitida and Lobitidae, and classed *Lobites*, with a query, in the sub-family Popanoceratinae. The same family was also taken to include *Megaphyllites* in 1913, whilst Hyatt, in 1900, had a family Megaphyllitidae, within the super-family Phylloceratida. I suggested in 1914 (p. 359) that a comparison of the development of the suture-line in *Megaphyllites* with that of *Monophyllites* did not reveal any connection of *Megaphyllites* and *Popanoceras* with the Monophyllitidae (already dealt with in Part IV). This view is still expressed in the present classification, but the Triassic *Parapopanoceras* is not now believed to be connected directly with the true Permian *Popanoceras*.

The family Joannitidae was separated from Arcestidae by Haug in 1894, but had been a sub-family in Mojsisovics already in 1882. This family has not been accepted by other authors, even by Hyatt (1900), who left the genus *Joannites* in the Arcestidae, as did Arthaber in 1927. The latter author, however, recognized a *Cyclolobus* group, after having, in 1911 and 1914, included *Joannites* in a sub-family Cyclolobinae. The same author's family Sphingitidae is here adopted, but it also was included again in Arcestidae by Arabu (1932).

A. Family ARCESTIDAE Mojsisovics (in Neumayr), 1875.

This family has been discussed so often, since it was first established, that it is impossible to repeat all that has been said for and against the subdivisions proposed at different times. The genotype of *Arcestes* itself is not yet fixed beyond Mojsisovics's (1893) statement that the group of the "*Arcestes galeati*" is typical. This would automatically make *Ammonites galeatus* Hauer (1846*a*) the genotype. This species was based on four different forms, according to Mojsisovics, but Hauer himself had mentioned that the ammonites represented in his pls. v and vi could easily have been referred to three or four different species, if less abundant material had been at his disposal. In 1850, however, after discovering that L. v. Buch had already used the name *Ammonites* *galeatus*, Hauer changed it to *Ammonites galeiformis*, without changing the circumscription of the species. As restricted by Mojsisovics (1875), *Arcestes galeiformis* (Hauer) thus is the genotype of *Arcestes* Suess, 1865. Arthaber (1914) seems to have been the first to state this in print, but Favre (1873*b*, p. 353) quoted *Ammonites galeiformis* Hauer as a typical example of *Arcestes* many years before.

Of the sub-genera established within the restricted *Arcestes* by Mojsisovics, all were listed by Hyatt (1900) as independent genera, but only *Proarcestes* was thus recognized by Arthaber in 1911, to which *Stenarcestes* and *Pararcestes* were added in 1926. *Ptycharcestes* was still included as a sub-genus by Diener in 1919, when he described a second " species " of this rather rare group. There does not seem to be any reason for treating this group, however doubtful, differently from the other sub-genera, and they are thus now all accepted as of equal status. These genera have since been increased by a few more, as mentioned below.

Arcestes s.s., then, comprises only the groups of *galeati*, *intuslabiati* and *coloni*, but they include a considerable number of species, and may yet be separated by future investigators as independent genera or sub-genera (see Arabu, 1924*a*). Owing to the fact that Arcestids in general are smooth and globose, the differences among Mojsisovics's groups are not as striking as are (perhaps less important) differences in the Trachyostraca on which some of the genera of Tropitida and Trachyceratida have been established. Thus, Diener (1925) defined *Arcestes* s.s. as including forms in which the varices were confined to the inner whorls, and in which the body-chamber became modified. On the other hand, in *Proarcestes* Mojsisovics, 1893 (genotype: *P. bramantei* Mojsisovics sp., 1869*b*), the inner and outer whorls remained essentially the same, both as regards whorl-shape and presence of constrictions or ridges. *Proarcestes* begins already in the Anisian, but *Arcestes* is typically later, while the *galeati* are confined to the Norian.

Pararcestes Mojsisovics, 1893 (genotype: *P. sublabiatus* Mojsisovics, 1875) has been described as intermediate between the first two genera, having a modified body-chamber, but retaining the varices of the earlier whorls also on the outer. Included in *Pararcestes*, at first, was Mojsisovics's group of the *carinati*, considered to be closely related to the *sublabiatus* group, but differing in details of the suture-line, notably the strikingly high median saddle in the external lobe. This group seems to be covered by *Galeites* Rollier, 1909, (genotype: *Arcestes carinatus* Hauer, 1892). Rollier's name was hidden away in a paper (1909) on Jurassic ammonites, in which he showed that carinate genera never gave rise to forms without a keel, whereas the reverse process was demonstrated in various groups, of which *Galeites* (arising from *Arcestes*) was one. Rollier did not introduce the name as new ; he did not mention a genotype ; and the name is not recorded in any of the standard indexes. As it cannot be applied to the *galeati*, i.e. the typical *Arcestes* itself, it may perhaps be found acceptable for the small *carinatus* group, however irregularly introduced.

Ptycharcestes Mojsisovics, 1893 (genotype : *P. rugosus* Mojsisovics, 1893) differs from all other Arcestids in having a body-chamber with radial ribbing. The unique type-specimen is possibly pathological and, in any case, looks abnormal ; but Diener (1919), in describing a totally different second species, referred to the close resemblance between *Ptycharcestes* and the genus *Lobites*. In the absence of the suture-line, Diener took the different shape of the aperture to be a distinguishing character ; but it is clear that *Ptycharcestes* is not, at present, a well-established genus.

Stenarcestes Mojsisovics, 1895 (genotype : *Arcestes subumbilicatus*, Bronn ; Hauer, 1846*a*) differs from the foregoing genera in its discoidal shape, with sometimes a spiral depression round the umbilicus or mere dimples, simulating ornamentation. There are certain peculiarities in the suture-line which may be mere mechanical adjustments to the flattened whorl-shape, and the range (from the middle Carnian to the upper Norian) is rather too considerable for *Stenarcestes* to be more than a morphological genus. The diagrams of the peristome of *Stenarcestes*, as of *Proarcestes*, *Pararcestes*, *Ptycharcestes* and the three groups of true *Arcestes* (*galeati*, *intuslabiati* and *coloni*) given in Arthaber (1927, pp. 47–51), will be found useful by the student of Triassic ammonites ; but they only emphasize the warning given by all authorities, that inner whorls of Arcestids are generally indeterminable.

The genus *Gonarcestes* Diener, 1919 (genotype : *Arcestes piae* Diener, 1919) was rather tentatively suggested for a single species that had its body-chamber modified in an unusual manner. It was described as resembling that of certain *Scaphites* of the Cretaceous in its double bend, but in its aperture and in the absence of constrictions or labial ridges on the final whorl, *Gonarcestes* agrees with the *intuslabiatus* group of *Arcestes* s.s.

Anisarcestes Kittl, 1908 (genotype: ? *Pararcestes subdimidiatus* Kittl, 1908) has lately been rediscussed by Johnston (1941), who described a doubtful Nevada form, comparable to Rumanian species recorded by Simionescu (1913). The open, *Sphingites*-like umbilicus is distinctive in the Nevada examples figured by Johnston, but they do not show the contrast between the strong folds of the body-chamber and the smooth inner whorls on which Kittl and Simionescu insisted in their diagnosis of *Anisarcestes*.

The genus *Rhaetites* Hyatt, 1900 (genotype: *Arcestes rhaeticus* Clark, 1887), according to Mojsisovics (1902*a*), is identical with *Arcestes* s.s. When Pompeckj (1895) re-described Clark's species he pointed out that the umbilicus of *A. rhaeticus* was very deep and funnel-shaped, and that the umbilical slope was separated from the side by an almost angular border, whereas in *A. gigantogaleatus* (with identical suture-line), that edge was blunt and rounded. This, however, is scarcely a generic distinction and the suture-line of a large *Rhaetites*, more recently figured by Andrusov (1934), also fails to show sufficient cause for Hyatt's separation of this genus from *Arcestes* s.s. The use of the name Rhaetitan for the Lower Rhaetic age was prompted by the lack of any alternative name.

The Klipstein Collection in the Museum includes the figured (and five other) examples of *Ammonites* (*Proarcestes*) *maximiliani-leuchtenbergensis* Klipstein (pl. vi, fig. 1), the first in an unusually good state of preservation. Like the minute original of *Ammonites* ? *labiatus* Klipstein and the figured specimens of *Ammonites quadrilabiatus* and *Ammonites latilabiatus* Klipstein (pl. vi, figs. 9, 3 and 8), they have been included in *Proarcestes bicarinatus* (Münster) by most authors; and there are three more specimens labelled "*Ammonites bicarinatus* M.," by Klipstein himself. *Proarcestes gaytani* (Klipstein) is represented only by a plaster-cast of the holotype, which was not examined by Laube. It is closer to Hauer's figure (1850, pl. iv, figs. 13, 14) than to Klipstein's, in side-view, but the septal surface in the latter's figure, like the terminal section in Hauer's illustration, shows a narrowing instead of a widening venter. The evenly rounded sides of the type are really subparallel and slightly divergent, not convergent.

Salter's Himalayan forms include six specimens of *Proarcestes bicinctus* Mojsisovics (= *Amm. diffissus* Hauer, in Salter, pl. vii, fig. 1, Nos. C. 4845*a–d* ; and pl. vii, fig. 3, Nos. C. 4844*a, b*) and three specimens of *P. ausseeanus* ? Hauer sp.(= Salter's pl. vii, figs. 2*a–c*, Nos. C. 4855*a–c*). There are also examples of *Arcestes leonardi* Mojsisovics from the *Halorites* Limestone of the Bambanag Section ; and specimens of *Arcestes* and *Proarcestes* from the *Tropites* Limestone of Byans and the exotic blocks of Malla Johar.

Apart from the many Anisian forms from Bosnia (V. Hawelka Collections, 1906–08, see p. 173), there are numerous examples of the same types from Montenegro (V. Hawelka Collection, 1926) ; but most of the many Arcestids from Timor and the Anisian of Nevada, as well as the Carnian of California, are not yet sorted or named.

The characteristic features of Arcestids in thin sections are the polygyral coiling and the comparatively close septation. These features, of course, have long been known in polished halves, and one of the best to be figured was *Stenarcestes subumbilicatus* (Bronn) in Hauer (1846*a*). Yet the spacing of the septa in Arcestids, close as it is, fails to impress when compared with that in some involute types like *Sageceras haidingeri*, or especially the gigantic *Pinacoceras metternichi* (Hauer) which has as many as 68 septa on the last chambered whorl. In the species of *Stenarcestes*, above mentioned, there are only 44 septa to the whorl and 37 before that, while two sections of the same species (from the Norian of the Raschberg), in the Museum (Nos. C. 1688*a, b*), show 46, 40, and 33 septa on three successive whorls at 75 mm. diameter, and 45, 35, 35, and 27 septa in the second example, at 61 mm. In a smaller specimen of *Arcestes intuslabiatus* Mojsisovics (No. C. 1664), comparable to that figured in Zittel (1884), there are 23 septa at 25 mm. diameter, and the whorl-height then is 20 per cent. This slow coiling is still noticeable in sections of the innermost whorls, e.g. the first three whorls of *Stenarcestes* figured by van Voorthuysen (1940, fig. 36, p. 96) but, of course, is not apparent in the very early stages (Branco, 1880, pl. x, fig. 6). This only shows the unusually large protoconch as the most striking characteristic, in addition to the subventral position of the siphuncle which, as a rule, becomes external soon after.

In six Timor examples of young *Arcestes* that were sectioned, the whorl-height at 20 mm. is 20 per cent., and only exception-ally 22·5 per cent. The number of septa is consistently high. One section, at 16 mm. diameter, shows 21 septa on the sixth whorl, increasing to 24 and 25 on the fifth and fourth, but decreasing to 22 on the third whorl. In another there are 23 septa on the two outer whorls at 23 mm. diameter, and in a third they are 22 each, at the same size. In still other sections the number of septa varies from an average of 16 for six whorls, to 17 on the second to fifth whorls, but only 16 on the sixth, while in one slide there are 17 at 20 mm., but only 16 on the next three inner whorls.

The close septation of the many-whorled Arcestids is thus a distinctive feature. In the somewhat similar Permian Cyclolobidae, e.g. in *Waagenoceras quadalupense* Girty (Miller and Unklesbay, 1943, pl. v, fig. 1) there are also 16 septa at one stage, in the third whorl, but only nine on the first two whorls. Moreover, that form has a very thick siphuncle, and though in other species of *Waagenoceras* the siphuncle is less massive, in *Arcestes* it is always thin. Unfortunately, in all the sections available the position of the siphuncle on the innermost whorls is uncertain. It is always external on the outer whorls and, according to v. Voorthuysen, it attains the ventral position already at the end of the second whorl.

B. Family JOANNITIDAE Mojsisovics, 1882, emend.

This family was first established as a sub-family and then included the Cladiscitids which were promptly separated by Zittel as an independent family ; also the Permian genus, *Cyclolobus* Waagen. This last was interpreted too comprehensively ; for Mojsisovics referred to it a Middle Triassic form from the Schreyer Alm which had simple, undivided saddles, so far as they are known. In *Procladiscites* the auxiliaries may be similar, but there are no comparable constrictions. The genus *Popanoceras* Hyatt (1883) was then also added to Joannitinae by Mojsisovics (1886) ; but Haug (1894), who raised the Joannitidae to family rank, objected and pointed out that *Popanoceras* could be looked upon as the ancestor of Arcestidae and had no place in the present family.

In view of the absence in the Lower Triassic of any forms that would bridge the gap between the Permian genus *Cyclolobus* and the first Anisian *Joannites*, it is here believed that the resemblance is superficial and that they represent independent stocks. For, after all, the resemblance is confined to the peculiar curve of the suture-line and does not apply to its various elements which are quite different. This curve is found in other specialized stocks and is not a primitive character; the similarity in this character is apparently quite accidental, as is the fact that two varices may be exactly opposite, which again causes resemblance to certain Permian forms. Arthaber, in 1927, discarded his family Cyclolobinae of 1911 and 1914 (here retained, Part IV, p. 19, for the Permian forms), and merely used the term "*Cyclolobus*-group," because a loose grouping, corresponding with stratigraphical facts, seemed to him preferable to a rigid classification into proper, systematic units. Could there be a stronger condemnation than this of the recapitulatory basis of classification which made Arthaber summarize the "*Arcestes*-group" only a few lines previously, as being "globose and involute in the young and possibly derived from the Permian *Waagenoceras*" ?

In the genus *Joannites* Mojsisovics, 1879*a* (genotype: *Nautilus cymbiformis* Wulfen, 1793) the smooth shell resembles that of *Arcestes*, but is generally more discoidal, with greater whorl-height and, as a rule, varices. The saddles of the suture-line, however, are not pyramidal but bifid or dimeroid, resulting, apparently, from a megaphyllic type. Johnston, who has more recently (1941) described the first Nevada species of *Joannites*, gave a useful diagnosis and a key to the recognition of species according to the number of varices per whorl, and the number of lateral lobes in the suture-line.

The genus is very well represented in the Collection, especially by Carnian species from the Hallstatt district. Many of these are from Mojsisovics's own collection. There are also representatives of some Spiti forms and of the various Timor species (unsorted). The Collection furthermore includes Klipstein's type of his *Ammonites multilobatus* (*non* Bronn, pl. ix, fig. 1) and a second, larger example, which is now decomposing. This species was renamed *Joannites klipsteini* by Mojsisovics (1882). There is a plaster-cast of the holotype of *J. johannis-austriae* Klipstein and four specimens (three of them the young of the same species ?) labelled *Ammonites partschii*. The largest example (of 13 mm. diameter) may be the figured specimen (pl. v, fig. 3), but its suture-line has the strong *Joannites*-curve and is not in the least like that represented in Klipstein's figure and description. But, as it is shown only in disconnected portions, it is possible that

Klipstein made up his drawing, perhaps partly from the two other, and more doubtful, specimens. The remaining (fourth) example is a *Nautilus*.

It may be mentioned that a thin section of a Hallstatt *Joannites diffissus* from Mojsisovics's own collection (No. C. 5603*a*), showed a smaller protoconch (·5 mm. instead of ·6) than that of the same species from Timor, published by v. Voorthuysen (1940). The siphuncle is external already in the second and third whorls, and there is, then, only slightly irregular coiling which quickly becomes a normal spiral. But the septa are much closer, for there are 18, 19, and 20 to the whorl on the seventh, sixth, and fifth volution, with 20 each on the next four successive inner whorls. There are about three constrictions to the whorl and they are independent of those on the earlier whorls.

The genus *Romanites* Kittl, 1908 (genotype: *R. simionescui* Kittl, 1908) is like *Joannites* in shape and has a similar suture-line; but it has spiral striation like *Cladiscites*, and no constrictions. Arthaber (1927) rightly pointed out that this type of ornamentation recurred in ancient groups; and he thought that *Romanites*, therefore, had best be considered to be a sub-genus of *Joannites*. The writer disagrees, and takes *Romanites*, known only from (presumably the Carnian of) Rumania, Greece and Timor, to be an independent genus, like the following interesting link between *Joannites* and yet another branch of the Leiostraca. This is the genus *Istreites* Simionescu. 1913 (genotype: *I. ptychitiformis* Simionescu, 1913), which shows a striking resemblance in shape to *Ptychites*. It is distinguished, however, by its bifid saddles, whereas the high and small external lobe again is different from the low and wide external lobe of *Joannites*. There are also no constrictions and no conspicuous curve in the suture-line.

c. Family SPHINGITIDAE Arthaber (1911), emend.

This family was established, not only for the typical predominantly Carnian genus *Sphingites* Mojsisovics, 1879*a* (genotype: *Ammonites coangustatus* Hauer, 1860), but for a variety of earlier genera, notably *Prophingites* Mojsisovics (1886), whose resemblance to *Sphingites* was previously (Part IV, p. 195) suggested to be merely a case of homoeomorphy. *Sphingites* is characterized by its open umbilicus which never contracts, and by the oblique constrictions or varices of its body-chamber. Hyatt, like most other authors, left *Sphingites* in the family Arcestidae. Haug (1894) was the only author who thought that the genus belonged to quite another series than that leading to *Arcestes*. *Sphingites* and its supposed "prototype" *Prosphingites*, however, were then confused, and apparently considered as synonyms in Haug's table of the Leiostraca (p. 394).

In his revised account of the genus *Sphingites*, Mojsisovics (1902*a*) recognized three different groups, the typical forms including five Carnian and one Norian species. Arthaber (1914) added a large but doubtful species from Asia Minor. *S. bacchus* Mojsisovics, with its barrel-shape, is distinct, and, according to its author, may yet be separated from *Sphingites* when its suture-line becomes known. *S. meyeri* (Klipstein), is a third isolated type, in Mojsisovics's opinion, and somewhat intermediate between the typical *coangustatus* group and the cadicone *S. bacchus*.

Klipstein's four examples of his *Ammonites meyeri* do not seem to include the figured holotype. The largest example, showing signs of decomposition, was originally larger than its present diameter of 8·5 mm., but as it includes half a whorl of body-chamber and Klipstein's figure has a septal surface at the end, it cannot have been the holotype, apart from the missing portion. A second specimen of 8 mm. diameter is typical, with its two constrictions, half a whorl of body-chamber on which the faint, *coangustatus*-ribbing appears, and suture-line with four or five saddles, as drawn by Laube and Mojsisovics. In a third still smaller example the two constrictions are very pronounced and wide, with the anterior margin sharply defined ; but the fourth example is a fragment of a very depressed Trachyceratid. Its Arpaditid suture-line, with two entire saddles, very wide lateral lobe, and only one auxiliary saddle is well shown ; the lateral and ventral incipient ornamentation, like the distinct, if shallow siphonal groove, are also well displayed, so that the inclusion of this fragment in *S. meyeri* is obviously due to some error. It may be the same form as *Ceratites brevicostatus* Klipstein (pl. viii, fig. 6), the holotype of which has a diameter of only 5·5 mm. This was included by Mojsisovics in *Trachyceras sulciferum* (Münster) but can be kept distinct, as in Laube's interpretation. Klipstein's three examples of *Ceratites sulcifer* include only one badly corroded ammonite of the same type, and two fragments of unrelated forms, possibly young *Klipsteinia* or " *Dinarites*."

Sphingites goldfussi (Klipstein) is based on four very small nuclei including the figured example (pl. vi, fig. 4). The much enlarged figure (× 5) is not very successful in peripheral view, but it is probable that the species is the young of *S. bacchus*. Since, however, the suture-line of that species is unknown, it is impossible to unite it with *S. goldfussi* which has the saddles only slightly less complex than those of *S. meyeri*. This may be due only to its small size. Klipstein's figure is not inaccurate in general appearance, though the details are somewhat diagrammatic.

D. Family CLADISCITIDAE Zittel, 1884.

Mojsisovics, in 1882, included *Cladiscites* and *Procladiscites* in the Joannitinae, but Zittel separated them from all the other Arcestids on account of their angustisellate primitive suture-line. The family has been accepted by most authors. Hyatt (1900) included in it the four genera *Cladiscites*, *Procladiscites*, *Paracladiscites* and *Psilocladiscites*, with *Hypocladiscites* as a sub-genus of the principal genus. This was still maintained by Diener in 1925, and Kutassy in 1933, but while admitting that the *tornatus* and *subtornatus* groups are very closely allied, I am listing *Hypocladiscites* as an independent genus, since it now includes a considerable number of species. Moreover, *Paracladiscites*, which is also listed as a sub-genus by Kutassy, has long been accorded generic rank by others. The family is more homogeneous than many others, with its rectangular whorl-sections, flattened sides and spiral ornamentation, but the suture-line varies from phylloid in the Anisian and Ladinian forms to an unusually deeply divided and slender type in the Carnian and Norian.

Even the microscopic characters of Cladiscitidae are fairly constant : a large protoconch (as in Arcestidae), but an external siphuncle from the beginning ; and a very thin siphuncle, unlike the Tropitidae (van Voorthuysen, 1940), but a thinner shell than the Arcestidae. Böhmer's (1936) statement that the internal structure of *Cladiscites beyrichi* showed great agreement with that of a Timor form of *Arcestes* was disputed by van Voorthuysen, who declared *A. bulla* of Böhmers to be a *Cladiscites*. In reality it could be argued that the sections of the inner whorls in the two stocks differ as much as the polished halves of large examples. For instance, the two specimens of *Stenarcestes subumbilicatus*, already referred to (p. 130), are entirely different from a polished half of a *Cladiscites* from the same deposit (Norian of the Raschberg, near Goisern, Austria) in the Collection (No. C. 1696). This has only 11 septa at 65 mm. diameter, increasing to 12 and 13 on the two next inner whorls, which brings the size down to only 13 mm. diameter when the whorl-height is still 30 per cent.

In a section of *Cladiscites* cf. *beyrichi* Welter, from Timor, at 24 mm. there are 15 septa on the two outer whorls, which agrees with the innermost whorls of (the possibly identical) *C. gorgiae* Gemmellaro, figured by v. Voorthuysen, and confirms the same author's contention that the number of septa, except in the first whorl or so, is fairly constant. The coiling, then, is only slightly less close than in Arcestids (whorl-height = 25 per cent. of the diameter), but in a section of *C. carinatus* Arthaber the proportion is already 32 per cent. at only 12 mm. diameter.

In order to discover whether the Anisian Cladiscitids differed from the typical Upper Triassic forms, five examples of *Phyllocladiscites crassus* (Hauer) were sectioned, but none of them showed the siphuncle on the inner whorls. The funnels of the last septate whorl are short and directed forwards, as well as backwards. The septa of the last chambered whorl number 15 in two sections, and 14 in one. The coiling is almost as slow as in the Arcestids, the whorl-height being 25 per cent. of the diameter ; but this feature also is not distinctive. In transverse section the deep umbilicus is striking, scarcely changing in width through the outer six whorls. The whorl-thickness is as much as 86 per cent. at 9·25 mm. diameter. The unequal thickness of the test is noticeable, changing from very thin at the umbilical suture to abnormally thick at the rounded umbilical border and the sides and venter.

The genus *Cladiscites* Mojsisovics, 1879*a* (genotype : *Ammonites tornatus* Bronn, 1832) is typically of Norian age, that is to say, it occurs plentifully with small and medium-sized specimens in the Middle Carnian, but ends with comparatively gigantic forms in the Upper Norian. *Procladiscites* Mojsisovics, 1882 (genotype : *P. brancoi* Mojsisovics, 1882) is one of the Anisian-Ladinian forerunners, with monophyllic, not dimeroid (or bifid) saddle-endings. *Hypocladiscites*

Mojsisovics, 1896*a* (genotype: *Cladiscites subtornatus* Mojsisovics, 1882) is typically Carnian. The smooth Cladiscitids without spiral ornament have been separated as *Paracladiscites* Mojsisovics, 1896*a* (genotype: *Ammonites multilobatus* Bronn, 1832). This genus includes the commonest Cladiscitid of the Norian in the Hallstatt Limestone and the commonest ammonite, or, indeed, fossil in all the Upper Trias of Timor. The Timor Cladiscitids are very well represented in the Collection, as are the Alpine and Bosnian forms, with a few from Spitsbergen,[1] India and New Zealand.

Psilocladiscites Mojsisovics, 1896*a* (genotype: *Procladiscites molaris* Hauer, 1887) of Anisian age was described as standing in the same relationship to the later *Paracladiscites*, as the early *Procladiscites* did to the Carnian-Norian *Cladiscites*. In other words, *Psilocladiscites* combines a smooth shell with the monophyllic saddle-endings of the equally Anisian *Procladiscites*, although this may persist into the Carnian. Later, however, Mojsisovics created the genus *Phyllocladiscites* Mojsisovics, 1902*a* (genotype: *Procladiscites crassus* Hauer, 1887), and this was considered the Anisian forerunner of *Cladiscites* itself, whereas Mojsisovics then took *Hypocladiscites* to be derived from *Procladiscites*. Diener (1915*a*) and Kutassy (1933) still listed *Phyllocladiscites* and *Psilocladiscites* as sub-genera of *Procladiscites*, though Mojsisovics (1902*a*) had considered it "entirely wrong to oppose the earlier Cladiscitids with phylloid saddle ending to the later true Cladiscitids, with bifid saddles." This, of course, would be no worse that what has been done in many other groups; J. P. Smith (1927*a*) and Johnston (1941), in any case, described species of Carnian age which are somewhat intermediate in suture-line. Much of the unnecessary complication was due to the establishment of sub-genera.

The Collection includes the original of Klipstein's *Ammonites ungeri* (pl. vi, fig. 7) and one syntype. The larger holotype shows extremely faint spiral lineation, but a more definitely Cladiscitid whorl-shape than Laube's or Mojsisovics's specimens; the suture-line is only partially exposed.

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[1] The uncrushed specimens from Cape Lee, Edge Island (N. L. Falcon Coll.) belong to the form figured as *Paracladiscites* cf. *diuturnus* Mojsisovics, by Frebold (1929) and came from the *Nathorstites* beds. One fine example is over 60 mm. in diameter.

E. Family MEGAPHYLLITIDAE Mojsisovics, 1896.

When separating *Megaphyllites* from *Pinacoceras* Mojsisovics (1879*a*) stated that he established the genus for the group of *Ammonites jarbas* (*Megaphylli* of Beyrich). Diener (1915*a*) thus quoted *Ammonites jarbas* Münster as the genotype, but since Beyrich's *Ammonites megaphyllus* seems to be the type by absolute tautonomy (Art. 30, I, *d*), Diener's selection might be questioned. J. P. Smith, in 1914, moreover, selected as type *M. sandalinus*, because it was the first species described by Mojsisovics; but though this designation has priority in date, Diener's selection of the only species associated with the genus in 1879, namely *M. jarbas*, must be accepted as binding, pending clarification of the position of *Ammonites megaphyllus*. Unfortunately, these two species are not even congeneric. Mojsisovics (1882) already thought that Beyrich's species, from an unknown horizon in Timor, with different lobes and a globose shape belonged to quite a different stock from his Triassic *Megaphyllites*. Subsequently, Welter (1915), who examined Beyrich's original, stated that it might be Lower Triassic but was not Ladinian or Permian. It is hoped that the continued use of *Megaphyllites* for the *jarbas* group will some day be sanctioned by the International Commission.

Mojsisovics in 1896(*a*) still included the Megaphyllitidae in the super-family Pinacoceratida, whereas Haug (1894) transferred the genus to the Phylloceratidae. Hyatt (1900) also adopted the family Megaphyllitidae, as a family within the Phylloceratida, for *Monophyllites* and other unrelated genera as well as *Megaphyllites*. In 1902, however, Mojsisovics repeated that *Megaphyllites* was a genus which died out without leaving any progeny, and could in no case be considered as the root-form of *Phylloceras*.

Megaphyllites was then included in Popanoceratinae (of the family Arcestidae) by Arthaber (1911 and 1914) and in the family Cyclolobidae Zittel, by J. P. Smith (1914), but these two families have been restricted to Permian forms in Part IV. On the other hand, *Parapopanoceras* Haug, 1894 (genotype: *Popanoceras verneuili* Mojsisovics, 1886) is now included in the present family. Mojsisovics (1902*a*), with an astonishing disregard for the laws of priority, attempted to restrict *Parapopanoceras* to the group of *P. hyatti*, and he proposed the new name *Dienerites* for the species with modified body-chamber. Since, however, Haug clearly designated *P. verneuili* as the genotype of *Parapopanoceras*, *Dienerites* falls into the synonymy. The unique *P. hyatti* Mojsisovics, on account of its radial folds and flattened whorl-shape, will have to be given a separate name, in spite of its comparative unimportance ; I am proposing for it **Ptychopopanoceras** gen. nov. (genotype : *Popanoceras hyatti* Mojsisovics, 1886, p. 67, pl. xiv, fig. 7). But it seems to me that the far commoner *P. haugi* differs still more from the true *Parapopanoceras* in its comparatively open umbilicus, its different whorl-shape, without sign of contraction of the body-chamber and a different suture-line. This, therefore, should also be designated with a distinct generic name, and I suggest **Neopopanoceras** (genotype : *Popanoceras* (*Parapopanoceras*) *haugi* Hyatt & Smith, 1905, p. 41, pl. xiii, figs. 1–22).

The reference, by J. P. Smith, of *Megaphyllites* and *Parapopanoceras* to two different families might suggest that the differences between them are more fundamental than appears at first sight. In the writer's opinion, however, this difference is partly due to the fact that, as already stated, the species attributed by J. P. Smith to the two genera are not typical, his "*Megaphyllites*" not even possessing a megaphyllitic suture-line. Apart from the irregular terminations of the lobes in *Neopopanoceras haugi* (Hyatt & Smith), which were taken to justify the recognition of a "*Popanoceras*-stage," the saddle endings are certainly phylloid, but not more so than they are, for example, in certain Acrochordicerates (Part IV, figs. 138, 139, pp. 401, 405). They are not nearly so distinctly megaphyllitic as in the original (and probably later) Spitsbergen *Parapopanoceras verneuili*, whereas the suture-line of the so-called *Megaphyllites septentrionalis* Smith is scarcely phylloid, much less megaphyllitic. The suture-line, in fact, might be compared to that of an Arcestid, e.g. *A. maximiliani-leuchtenbergensis*, in Branco (1879, pl. vii, fig. 1), but not to the suture-line of a *Megaphyllites*, e.g. the same author's *M. insectus* (*ibid.*, fig. 4). In this connection it may be mentioned that one of the most typical megaphyllitic suture-lines known is found in *Phyllocladiscites macilentus* (Hauer), as figured in Tommasi (1899*a*, pl. iii, fig. 8).

In thin sections *Neopopanoceras haugi* shows a siphuncle that is external from the start, as in the Permian true *Popanoceras*. Since all Permian ammonoids, so far sectioned, however, have an external siphuncle, with the exception of *Agathiceras* and *Neoaganides*, and since the majority of Lower Triassic ammonites have a similarly external siphuncle, this feature, by itself, is not of any diagnostic value. The width of the siphuncle is 1·25 mm., or one-fifth of the diameter of the third whorl, and the long siphonal funnels are then still directed backwards ; but on the outer whorls of all the six sections, up to 10 mm. diameter, the funnels are directed both forwards and backwards. On the innermost three whorls there are 14, 15 and 16 septa in one slide, and 14, 19 and 19 in another, as against 9, 11 (?) and 11 (?) in *Popanoceras annae* Ruzhenčev, as figured in Miller & Unklesbay (1943). Only one feeble constriction could be seen on one of the specimens, and none of the initial constrictions was clearly developed.

Whether the genus *Nitanoceras* McLearn, 1937*a* (genotype : *Arcestes* ? *selwyni* McLearn, 1930) should be included here is altogether doubtful. I (1933*b*) criticized the creation of this 'species,' based on a form described as having a "ceratitic" suture-line, yet referred to the genus *Arcestes*, even if marked with a query. The illustration is useless and certainly does not suggest a Megaphyllitid. On the other hand, in 1937(*a*), it was described as smaller, with a simple suture-line of fewer elements than any species of *Megaphyllites*, while also smaller, even more evolute and with a simpler suture-line than any of the Spitsbergen species of *Parapopanoceras*. The description of the suture-line, with its eight lobes, reads like that of *N. haugi* at a diameter of about 11 mm. (J. P. Smith, 1914, pl. xiii, fig. 10), but with more auxiliaries. That, however, is a mere guess.

Megaphyllites is well represented in the Collection, especially by Anisian forms from Bosnia. In the Klipstein Collection from St. Cassian there are five poor examples labelled "*Ceratites jarbas, M.*" and six marked "*Ammonites umbilicatus*, nob." The original of Klipstein's figure (pl. vi, fig. 5) could only be the large specimen (of 34 mm. diameter) which is mentioned in the text (p. 118), and which may have been utilized in preparing the figure, although Klipstein states that it was received "later." The other examples are more inflated in proportion, and probably identical with *M. jarbas*, as Laube suspected. The unusual compression of the large specimen, however, and of the original figure, is due to crushing in the rock, so that the species *Ammonites umbilicatus* may safely be disregarded.

A number of specimens of the Bosnian *Megaphyllites* *sandalinus* Mojsisovics were sectioned and they show a siphuncle which is external from the start, with the funnels (directed backwards) rather long on the second and third whorls, but shorter and directed forwards as well as backwards on the fourth and fifth whorls. In *Monophyllites*, which also has an external siphuncle, the funnels are directed both ways at a much earlier stage, and no long funnels were observed. The protoconch is large (·5 mm.) as in *Arcestes*, but the number of septa varies ; in one section there are 9, 13 and 14 on the first three whorls, in another 11 on the first, and in still another slide the septa are very closely spaced on the second and third whorls.

F. Family NATHORSTITIDAE nov.

This family is established for the single genus *Nathorstites* J. Böhm, 1903 (genotype : *Popanoceras mcconnelli* Whiteaves, 1889), whose systematic position has puzzled observers to the present day. Most of them agreed that it was out of place in the Permian family Popanoceratidae ; and Mojsisovics (1896*a*) thought that it represented a new Arcestid type with prionidian lobes whose stratigraphical position had yet to be elucidated. This view was echoed by Diener (1916*c*), who spoke of it simply as an Arcestid. Smith (1927*a*) again referred the genus to Popanoceratidae, although Mojsisovics had already expressed his opinion that *Nathorstites* could not be classed with the Anisian so-called *Popanoceras*.

While generally accepting the view that *Nathorstites* was an Arcestid and a possible derivative or companion of (the equally Ladinian ?) *Parapopanoceras*, the writer was struck by its resemblance to certain keeled Hungaritids, and *Neodalmatites* (see p. 23) in particular. *Nathorstites*, of course, agrees with Arcestids, including *Parapopanoceras*, in having a long body-chamber (one whorl or more), as distinct from the microdome *Hungarites*. But Diener (1915*a*, 1925) had shown that there was no reason why a form with short body-chamber should not give rise to a macrodome successor ; for example, no one questioned the derivation of the longidome *Costidiscus* from the brevidome *Lytoceras*.

The possibility of *Nathorstites* being connected with a keeled stock was thus ever present, as will be seen from the following observations on the genus, based on considerable material, including thin sections.

On dissecting *Nathorstites* to the innermost whorls, a certain resemblance to young Arcestids is obvious, but the general aspect is less spherical, because the umbilicus is more open, as in the inner whorls of *Tropites*. The whorl-section, however, is depressed, reniform, with a rounded umbilical border. Conversely, the nucleus of *Neodalmatites* at 2·7 mm. (Smith, 1914, pl. xxx, figs. 10–12) is much less globose and has a still wider umbilicus, apart from the ribbing which rather contradicts any resemblance there may be in other characters. The suture-line, again, is straight and serial in *Nathorstites*, as in young *Arcestes*, only there are fewer elements in the former. In the young *Arcestes pacificus* Hyatt & Smith, at 2 mm. diameter (Smith, 1927*a*, pl. xxiii, fig. 23), there are already four saddles in the external suture-line, outside the umbilical saddle. In *Nathorstites*, at 4 mm., there are only six similar saddles in the whole suture-line, external and internal, but they show the same proportions, with the external and first internal saddles decidedly the largest. Subdivision of the external and first lateral lobes does not appear until a diameter of about 15 mm. is reached, when there are six saddles, including the umbilical saddle, on the external half of the straight suture-line.

In the adult *Nathorstites* the ventral lobe is bordered by the subparallel sides of the still rather large external saddles which, however, are no longer dominant. These are followed by the principal lobe, which is generally the largest. The curvature seems to vary ; it is quite pronounced in some suture-lines figured by Böhm and in Diener's Kotelny form, but in the Spitsbergen examples the suture-lines seem to be more or less straight. In large specimens of *Nathorstites* from Edge Island, and in the Bear Island *N. lenticularis* (Whiteaves) figured by Böhm (1903, pl. vii, fig. 14), the two branches of the external lobe became toothed, but not in other examples (e.g. Böhm's fig. 12). The succeeding saddle may be even less wide than the next following saddle, but there is no suggestion of an adventitious lobe as in *Neodalmatites*.

The unkeeled *Nathorstites alaskanus* Smith (1927*a*, p. 67, pl. cii, figs. 11–13) and some comparable inflated Edge Island specimens, probably *N. gibbosus* Stolley, var. *globosa* of Frebold, have the same type of suture-line with fewer elements, i.e. 3–4 saddles up to 15 mm. diameter. But in a large example of *N. concentricus*[1] from Mt. Congress (Dixon Land) there are eight saddles in the external suture-line, all more rounded and shorter than in the equally large examples, presumably of *N. lenticularis*, from Edge Island. Moreover, the lobes are spreading at the expense of the saddles so as to cause a feebly megaphyllitic aspect. Since they are of Ladinian, if not Anisian age, they are decidedly in favour of a megaphyllitid origin of *Nathorstites*, presumably by way of *Parapopanoceras*. On the other hand, the reputed Carnian forms of *Nathorstites*, with their simplified suture-lines, are undoubtedly very closely connected with their probable forerunners, agreeing in every feature, including the course of the radial line.

The striae of growth in *Nathorstites*, whether from Spitsbergen or British Columbia, are strongly recurved on the outer half of the whorl-side, and they go across the sharpened periphery almost in a straight line. Whiteaves's original figures do not show this striation, but it can be seen in one of J. Böhm's Bear Island examples of *N. lenticularis* (pl. vii, fig. 6). There is a lateral lappet to the aperture, as in the form figured by Stolley (1911, pl. ix, fig. 1), and the curve is essentially the same as in *Neodalmatites parvus* Smith sp. (1914, pl. xxx, fig. 1), with the usual folds more or less developed in all *Nathorstites*. It may be added that the concentric lineation, suggestive of that in *Otoceras* (Spath, 1930, pl. i, fig. 1*c*), is found also in most *Nathorstites*, as in some Hungaritids, especially again *Neodalmatites*. In at least some of the examples of *Nathorstites* there is oblique striation in between the spiral lines, suggestive of that peculiar type of ornamentation found in some *Placenticeras* and *Oppelia* of much later date.[2]

The similarity of *Nathorstites* to *Neodalmatites* in whorl-shape, ornamentation, and suture-line seems, thus, to be accidental and not due to genetic affinity. On the other hand, direct connection with *Parapopanoceras* cannot yet be established. There is a single form from Edge Island (Cape Lee), from lower than the great thickness of *Nathorstites*-

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[1] In 1921 (p. 351) I thought the resemblance of the crushed Spitsbergen "*Ptychites*" *concentricus* (Öberg) to the oxycone *Nathorstites* was due to deformation in the rock. But larger and fairly well preserved examples have since been received of up to 60 mm. in diameter and showing the characteristic *Otoceras*-like concentric ridges.

[2] See Wepfer, (1920, p. 339). A presumably similar kind of striation was referred to by J. Böhm.

bearing " Purple Shales," which has no keel and looks like the inner whorls of *Parapopanoceras verneuili* Mojsisovics, but the body-chamber is badly crushed. Only its suture-line is not more megaphyllitic than that of the Middle Triassic *Nathorstites* from Mt. Congress, Dixon Land. A second example is a globose nucleus, too immature to be helpful, and the associated ammonites are a few small and indeterminable *Gymnotoceras* (?). If *Nathorstites* be derived from *Parapopanoceras*, by simplification of the suture-line, and acquisition of a keel, the latter probably first appeared on the inner whorls, which are more distinctly carinate in the early Mt. Congress forms, as already mentioned. It should be added that a Peace River (British Columbia) example of *Nathorstites mcconnelli* (B.M., No. C. 39724) also has a rather massive keel, not merely a sharpened periphery.

It will be seen that there are serious objections to including the isolated genus *Nathorstites* in either Arcestidae or Megaphyllitidae, for, although an ephemeral keel is not unknown in the former family, its suture-line is highly complex, not simple. *Megaphyllites* has a phylloid suture-line already at a very small diameter (2·5 mm.) ; and the keeled *Nathorstites*, with its simple suture-line, would seem to be equally out of place in the unkeeled family Megaphyllitidae. The New Siberian (Island of Kotelny) form of *Nathorstites*, recorded by Diener (1916), again has a rather peculiar type of elongated megaphyllic saddle, quite different from the short and rounded saddles of *Parapopanoceras*. In the circumstances it seems best to establish a separate family.

The *Nathorstites* material in the Collection includes the crushed *N. concentricus* (Öberg), recorded by the writer in 1921 (p. 351) from Sassen Bay, Ice Fjord, Spitsbergen (W. J. Reynolds Coll., B.M., Nos. C. 22047–22058), which may include both *N. tenuis* and *N. gibbosus* Stolley. An uncrushed example of the latter "species," labelled Ice Fjord, was collected by Mr. R. W. Segnit (B.M., No. C. 37233). Then there are the Mt. Congress specimens already mentioned, which were collected by members of the English-Norwegian-Swedish expedition to Spitsbergen in 1939. A surprising feature was the association of these *Nathorstites* in the same[1]

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[1] The same hand specimen (with a small, globose *Ptychites* and *Nathorstites*) included what may be a young extreme of that genus, which has very depressed whorls, lateral tubercles and a broad *Tropites*-keel, with accompanying furrows. It is a far more convincing ancestor

hand-specimens with *Monophyllites* (? *Ussurites*) *spitsbergensis*, *Ptychites trochleaeformis* (Öberg) and more globose young of *Ptychites*. This indicates an age not later than Ladinian, and they may thus well come from a horizon near that of *Neodalmatites*.

The many pyritized specimens from Cape Lee, Edge Island (N. L. Falcon Coll.), came from a bed in the " Purple Shale Series " (*Daonella* shales) and were associated with Cladiscitids. But at Keilhau Bay, in the south of the island, the numerous, more or less crushed examples of *Nathorstites* were in clay-ironstone nodules from a range of about 200 feet in the same shales.

The only other specimens are *N. mcconnelli* and *N. lenticularis* from the *Nathorstites* zone of the Schooler Creek Formation, near Beattie Ranch, Peace River, British Columbia, collected by Mr. F. H. McLearn. These were associated with the presumed Ladinian or Lower Carnian ammonites, discussed on p. 42.

X. Super-family PTYCHITIDA Mojsisovics 1882, emend.

When Mojsisovics first established a sub-family Ptychitinae, he included in it a number of genera which later authors thought very heterogeneous elements. Thus, Zittel (1884) was at a loss to give a diagnosis for this assemblage which he raised to the rank of a full family. But he still included in it various leiostracous and trachyostracous genera which, one by one, were transferred to other families or super-families. Finally, even *Sturia* was placed by Mojsisovics in the family Gymnitidae, and *Nannites* into the super-family Ceratitida, so that only *Ptychites* itself was left of the original genera.

Meanwhile Hyatt (1900) had added to *Ptychites* (in his own family Ptychitidae) the genera *Japonites* and *Pseudodanubites*, both of which, however, are here excluded from the family. The former (see p. 171) is now referred to

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of the Tropitidae than the Eotriassic *Protropites*, with its ephemeral keel; but the costation is strongly recurved, as in *Nathorstites*, and crosses the periphery in a slight sinus, concave forwards. There is spiral ornamentation all along the side. None of the gibbose young of the Edge Island forms of *Nathorstites* has a similar *Tropites* keel though the young of *N. concentricus* are apparently more comparable in that respect, before the periphery sharpens in the adult.

Gymnitidae; the latter is here included in the family Danubitidae (p. 14). Arthaber (1911) and J. P. Smith (1913), after Waagen (1895), added the Lower Triassic genus *Proptychites*, for which a separate family-name was adopted in Part IV (p. 164). It was then pointed out that the Meso-Triassic *Ptychites*, with its Arcestid inner whorls, was not directly descended from the Proptychitidae. Arthaber's second subfamily within the Ptychitidae, namely the Gymnitinae, are discussed below, under the super-family Pinacoceratida. But it is interesting to note that the Gymnitinae were made to include *Proteusites* Hauer, whereas J. P. Smith referred this genus to the Ptychitidae and not to his Gymnitidae. This genus *Proteusites* also has already been dealt with (p. 31), likewise the inclusion, in Gymnitidae, of the genus *Monophyllites* (see Part IV, p. 285). There remains thus, in the Ptychitidae, only the genus *Ptychites* itself, but, with Diener (1925) and Arthaber (1927), I am including here *Sturia* Mojsisovics. J. P. Smith, it may be mentioned, misidentified the latter ; and the Nevada *Ptychites* he described are not the same as the common European and Asiatic true *Ptychites*.

Most authors noticed the globose whorl-shape or even depressed whorl-section of young *Ptychites* (wrongly called the " *Nannites* " stage, see p. 160), and the resultant similarity to Arcestids. There is some resemblance also to young *Proteusites*, as mentioned before, but the family, on the whole, are believed to be related to the stock that also gave rise to the Arcestidae and the Megaphyllitidae. Like the Phylloceratida they are probably derivatives of the Meekoceratida in the wider sense, and I consider it futile to trace them back to a Devonian goniatite family like the Tornoceratea, or even the Carboniferous *Gastrioceras*, when the Lower Triassic forerunners are still so incompletely known.

A. Family PTYCHITIDAE Mojsisovics, 1882.

The genotype of *Ptychites* Mojsisovics, in Neumayr (1875), is said to be *Amm. eusomus* Beyrich (1865). Of Mojsisovics's five original groups of 1882, the group of *P. rugiferus* (Oppel) was described as the fundamental stock with a tendency to conserve the original thick and globose form. The other branches were so many variations, diverging in different degrees and in different ways from the *rugiferus* " prototype."

As the first species described in 1882, namely *P. eusomus*, selected as genotype by Diener (1915*a*), belongs to this *rugiferus* group, there is little doubt as to the interpretation of the typical forms.

Yet, from a purely systematic point of view, a case could be established for selecting *Amm. rugifer* itself as the genotype, for it was one of the original species quoted in 1875. It is true that Mojsisovics stated that *Ptychites* was equivalent to Beyrich's group of "*plicosi*" and Oppel's group of *rugiferi*; nevertheless, none of Beyrich's species is among the six examples listed, and, since these are the first species connected with the name *Ptychites*, the genotype should have been selected from that list and not from the species described seven years later. This may be considered by some future nomenclator as a formal selection of *Amm. rugifer* instead of *Amm. eusomus* as genotype of *Ptychites*, but, pending a decision by the International Commission, Diener's selection, of course, has priority.

The development of the suture-line in *Ptychites* was not recorded by Branco who only figured the protoconch. This was described as angustisellate (erroneously marked latisellate on the plate) and resembled that of *Megaphyllites*. Few observations seem to have been made since, but Arthaber pointed out that in the young the saddles were still ceratitic, with a notch first appearing in the second lateral saddle. J. P. Smith (1932) stated that the late larval stage of *Ptychites seebachi* Mojsisovics greatly resembled *Proteusites*. Since he also said that the young stages of the latter genus and the allied "group of *Ceratites decrescens*" had not been described, Smith must have meant the adult *Proteusites* resembled the young *Ptychites*. At the same time he admitted that the group was only "apparently" more nearly related to *Ptychites* than to the Haloritidae. This was scarcely an advance on what Kraus had written about *Proteusites* and allies sixteen years before.

What struck me, in my own investigations of the early stages of *Ptychites*, was the globosity of the nucleus, even in the forms with comparatively open umbilicus, like *P. seroplicatus*, *P. pusillus*, and *P. patens* Hauer; the large number of elements of the suture-line, both external and internal; and the large median saddle in the external lobe. In the three species just mentioned, few unbiassed observers would consider this lobe to be represented by the two notches at the summit of the median saddle (simple incisions in the case of the last two, but subdivided in *P. seroplicatus*), and would use the term external lobe for the wide and often largest lobe on each side of the massive median saddle. Hauer, indeed, did call these incisions the external lobe, which he described as so shallow, and hence the external saddle so small that they could well be interpreted as mere parts of a large median saddle. Mojsisovics had stated already in 1882 that he had formed the opinion that the short external saddle of *Ptychites* was an element derived from the median saddle in the external lobe, which had become individualized in the course of time. Zittel's diagnosis, therefore: " siphonal lobe very shallow, external saddle strikingly short, first lateral saddle very high . . .", applies to the typical species, e.g. *P. domatus* and *P. suttneri* (sic) as figured in Mojsisovics, less so to *P. seroplicatus*, and not at all to *P. pusillus* or *P. patens*.

On the other hand, the development of the suture-line of the Ladinian *P. noricus* Mojsisovics, as published by Bubnoff (1921), reveals the presence of a normal median saddle in the external lobe from the beginning, also a short external and a high lateral saddle which did not seem to vary much in ontogeny. This is not an arrangement peculiar to late forms of *Ptychites*, for a similar suture-line is found in the large Anisian *P. multiplicatus* Hauer from Bosnia. All the forms I dissected had a large median saddle in the external lobe, about half as broad again as that of *Arcestes* (*Proarcestes*) *carpenteri* Smith (1927*a*, pl. xxiii, fig. 10), and distinctly tripartite at the apex. At the same diameter (4 mm.) the saddles are slender and so finely subdivided that it is difficult to say whether they are already entire, but there is no suggestion of a ceratitic appearance or a contraction of the saddles at the waist or near the base. In the inflated forms the saddles are not so slender as in the more compressed types, and in both there are about six external and five internal saddles, at 5 to 7 mm. diameter.

In one Bosnian example, at 4 mm. diameter, the tripartite median saddle in the external lobe is comparable to that of *Agathiceras sundaicum* Haniel (as figured in Böhmers, 1936, p. 56, text-fig. 37*k*) and the adjoining lobes are deep and bifid, but the smaller and higher lateral lobes are trifid. In another globose Spitsbergen form the wide siphonal saddle has a median cleft in the siphonal line so that it resembles the median saddle in the suture-line of *Beloceras multilobatum* (Beyrich), as figured in Branco (1880, pl. vi, fig. 6*d*).

The appearance of the median saddle, then, in the young, just described, is that of the typical *P. rugiferus* and it is well illustrated in the peripheral view of *P. domatus* Mojsisovics (1882, pl. lxii, fig. 4*b*). But it seems to be independent of whorl-shape and ornamentation, and while it would be simple to keep the *rugiferi* distinct from the well-known *flexuosi*, and these again from *Discoptychites megalodiscus*, on account of the proportions of their saddles and their number, there are many intermediate types like the common *P. gibbus* Mojsisovics (1882, pl. lxv, fig. 2). It should be added that there is nothing in *Ptychites*, so far as I know, that could be compared to the tripartite, wide, median saddle in the external lobe of *Arcestes* (*Proarcestes*) *shastensis* Smith (1927*a*, pl. xxii, fig. 26) at 1·3 mm. diameter. I have not been able to dissect *Ptychites* down to a comparable size, but the Californian Arcestid reverts to a simple external lobe already at 2·25 mm., and, of course, there are no adventitious elements in any Arcestid. The recapitulatory value of this tripartite median saddle is therefore entirely problematical.

The observations made on thin sections are not much more decisive. A median section of *P.* cf. *oppeli* Mojsisovics, I made many years ago, missed the siphuncle but showed the presence of numerous constrictions on the inner whorls, up to about 5 mm. diameter. As in actual specimens of the same size, the constrictions are not visible externally, so in thin sections they are seen to be developed only on the cast. The siphuncle in other sections is external from the start, as figured in Schindewolf (1934, 1941), and although it is fairly thick, this is connected with the low whorls and can be compared to the siphuncle of *Joannites*, figured by van Voorthuysen (1940). The siphuncle of other Arcestids figured by the same author is not quite external at the start, but Böhmers (1936) figured a section of *Arcestes bulla* Arthaber,[1] which shows the siphuncle to be external from its first appearance. In one section the funnels can be seen to be directed forwards, without any backward extension, as in *Proteusites*, but it is uncertain whether this applies also to the innermost whorls.

The group of *Ptychites megalodiscus*, Beyrich sp. (1867), has

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[1] According to van Voorthuysen (1940, p. 102), the form described by Böhmers as *Arcestes bulla* is a species of *Cladiscites*.

been separated as *Discoptychites* by Diener (1916*e*). It was originally characterized as including forms which already in the young stages had a strongly raised umbilical border. This was said to distinguish them from all other Ptychitids, but it is probable that Diener, in creating *Discoptychites*, had in mind both the discoidal forms, like *P. megalodiscus* and *P. evolvens* Mojsisovics, and his own *P. fastigatus*, with a sharp keel as well as a closed umbilicus. A striking feature of the suture-line is the presence of a small adventitious element in the external lobe.

The *subflexuosi* and *flexuosi* differ merely in the number of lateral lobes, but agree in their flattened whorls, often with a moderately open umbilicus, and a comparatively low umbilical wall. Since these *flexuosi* have often been represented as typical *Ptychites* in the more general text-books, it may seem unnecessary to some to separate them from the *rugiferus* group with an independent name. Yet all the other groups have now been renamed, with the exception of the *opulentus* group, which agrees with the typical *P. rugiferus* in all features but the number of lateral lobes; and the new name, **Flexoptychites** gen. nov. is therefore now proposed, type to be *Ptychites flexuosus* Mojsisovics (1882, p. 261, pl. lxiii, fig. 2). This group passes up into the Ladinian, with *F. noricus* (Mojsisovics) which, however, is already transitional to *Alloptychites*, mentioned below. An abnormal form of this group is *P. charleyanus* Diener, with a strong keel and a very simple suture-line.

Two more groups of *Ptychites* were recognized by Diener in 1895(*b*) and later separated with independent names. They are *Aristoptychites* Diener, 1916*e* (genotype : *Ptychites gerardi* Blanford sp., 1863), which has trigonal whorls, is gradumbilicate, and has much feebler folds than the true *Ptychites*. The suture-line has also been described as differing from that of all other Ptychitids in its curvature, but this is not very conspicuous in one of two examples (of Salter & Blanford's *Amm. gaytani*, 1865), which shows the suture-line (B.M., No. C. 4859*a*), nor in a large Spiti example (No. C. 28623) named by Diener himself, which is still septate at a diameter of about 100 mm.

The second genus is *Malletoptychites* Diener, 1916*e* (genotype : *Amm. malletianus* Stoliczka, 1865), which has a wide umbilicus and trigonal whorls, and a peculiar suture-line, resembling that of *Japonites*, but still with the typical *Ptychites* median saddle in the external lobe. Like the other genera proposed by Diener in 1916, more or less tentatively, and completely disregarded by all authors, including Kutassy, the above Ptychitidae are now accepted as independent genera.

To these may be added **Alloptychites** gen. nov., proposed for *Ptychites meeki* Hyatt & Smith (1905, p. 87, pl. xxv, figs. 6–12). This has a wide external lobe, with a median saddle and no suggestion of an adventitious element. There is also only comparatively fine striation, rather irregular and quite different from the coarse plication of the typical *Ptychites*, even in the comparatively more distinctly costate young. The simple suture-line, however, is its most distinctive feature.

The genus *Ismidites* Arthaber, 1914 (genotype: *I. marmarensis* Arthaber, 1914) was described as of uncertain systematic position and of unknown age, but it does not look out of place in the Bithynian fauna, which is preponderantly Anisian, and a fair selection of which is in the Museum. *Ismidites* looks much like *Ptychites* and the blunt ribs are not more falcoid than in some of the *flexuosi*, but the umbilical edge is distinct, as in *Alloptychites* or the Indian *Aristoptychites gerardi*. The suture-line, however, is peculiar and caused Arthaber some difficulty. He compared it to the not very dissimilar but longer suture-line of *Proptychites*, but thought that the suture-line of *Trachyceras*, e.g. *T. scaphitoides* Mojsisovics showed more resemblance. This, of course, is purely fortuitous, as all other characters differ fundamentally.

The normal *Ptychites* suture-line has two lateral lobes and several auxiliaries, but it can be much shorter. The suture-line of *Malletoptychites*, for instance, shows some resemblance to that of *Ismidites*; and at least in the proportions of the small external (or adventitious) saddle and the large lateral saddle it is more in agreement than the presumed comparable *Trachyceras* suture-line figured by Arthaber. It is true that in *Ismidites*, which has a small umbilicus, the suture-line is short, whereas in *Malletoptychites*, with an open umbilicus, it is longer when it would be expected to be the other way about. But if there were complete agreement, Arthaber would have discovered it. Since comparison with *Beyrichites*, or any other externally similar genus, is much less feasible on account of the suture-line, *Ismidites* is included in the present family.

The genus *Ptychites* in the wider sense is well represented in the Museum. Apart from many Alpine examples, a number of which came from Mojsisovics's own collection, there are the 640 Bosnian specimens recorded by the writer in 1921 (Spath, Spitsbergen, *Geol. Mag.*, p. 348), a dozen of which were sectioned. As has been mentioned by Gugenberger (1927), by far the commonest species on Volujak Mtn. are *P. flexosus* and *P. acutus* Mojsisovics, with many gigantic forms. The Collection has since been enriched by many Montenegran specimens. There are also various Spitsbergen and Himalayan species, the latter examined by Suess as long ago as 1862.

The genus *Sturia* Mojsisovics, 1882 (genotype: *Amaltheus sansovinii* Mojsisovics, 1869*b*) shows as much as any other genus of ammonites how interpretations may vary. Zittel's (1884) definition: "Shell as in *Ptychites*, but with spiral striae," was as clear and concise as Diener's diagnosis of 1925. Yet in the meantime Mojsisovics had included *Sturia* in the family Gymnitidae rather than Ptychitidae, provisionally, it is true, and on what seems to the writer a superficial resemblance to the Eotriassic genus *Ussuria* Diener. Then, even before Waagen (1895) stated that *Sturia* was very closely allied to *Ptychites* and that that relationship had never been questioned by anybody, Haug (1894) thought that *Sturia* and *Gymnites* were nearer to *Cladiscites* than to Ptychitinae. This he followed up by a complete separation of the Ptychitidae and Cladiscitidae from the Gymnitidae (1907). Mojsisovics (1902*a*) himself had become somewhat uncertain concerning the affinities of *Sturia*, and was impressed by the similarity of its suture-line to that of *Procladiscites*; and this view was echoed in 1934 (Part IV, p. 164). As Arthaber (1914) pointed out, however, the resemblance between certain of the less compressed types of *Sturia* and *Procladiscites* of the same beds was a case of homoeomorphy, the broader venter, regular, spiral striation, and shape of the saddles distinguishing the latter genus.

Still other views have been expressed. Hyatt, in 1900, seems to have missed out *Sturia* altogether, but in 1905, he and Smith included that genus in the family Thalassoceratidae (typically Permian), together with *Ussuria* (see Part IV, p. 212). Smith, in 1913, still followed this classification, but in 1914, Arthaber put *Sturia* back in its proper place in the Ptychitinae.

The writer is thus accepting *Sturia* as a genus of the present family on the basis of its globose and constricted young stages and the general agreement in the internal characters as seen in micro-sections; the discoidal shape recalling that of *Discoptychites*, with obscure radial folds; and the general resemblance in the suture-line. I also agree with Arthaber (1927) in considering *Sturia malayica* Welter (1914) as misidentified. It is a Juvavitid whose resemblance to *Sturia* is purely accidental but curiously close. The presumed *Sturia* of Smith's latest work (1932) have already been dealt with in Part IV, pp. 213, 214.

The stratigraphical range of *Sturia* is unusually long; it is common in the Anisian, but persists through the Ladinian into the Carnian. The Collection includes various forms from Alpine, Anatolian, and Himalayan localities, and a particularly large number of the typical *S. sansovinii* and *S. arata* from Stavljan, Volujak Mtn., Bosnia. I have been able to make sections of some duplicates, and the inner whorls do not seem to differ much from those of *Ptychites*, except that the constrictions are not so conspicuous. There are about thirty septa in the first 2½ whorls, and the siphuncle is external from the start.

The Bosnian *Sturia* (?) *gracilis* Hauer is characterized by a very peculiar and straight, multisellate suture-line, so that at first it was also doubtfully attached to *Pinacoceras*. There are no adventitious lobes, apparently, as in the typical Pinacoceratidae, but the presence of at least seventy-two elements in the suture-line rivals the acme of ammonite specialization in that family. There is also no indication of even a curve in this unusually long suture-line. Since there are about thirty septa on the outer whorl of the holotype, at only 20 mm. diameter, there must have been more than the usual interference among neighbouring septal edges to cause forward or backward deflection, yet the elements kept in a perfectly straight line. Hauer did not find any spiral striation, but, of course, this could have developed at a larger size. The suture-line, however, is distinct enough for separation of this small Bosnian form from the megalomorph *Sturia* and the new genus **Metasturia** gen. nov. is now proposed for it (genotype: *Sturia* (?) *gracilis* Hauer, 1892, p. 283, pl. x, fig. 8). The contemporary (Anisian) Pinacoceratids, i.e. *Parapinacoceras*, are clearly distinguished by their adventitious saddles.

The genus *Psilosturia* Diener, 1916*e* (genotype: *Sturia* *mongolica* Diener, 1895*b*) differs again in its suture-line, the pyramidal saddles being unusually long and slender, but the wide external lobe with its large median saddle is still typical. The suture-line as a whole was considered by Diener to be on a somewhat lower level of development than that of the Alpine species of *Sturia.* The umbilicus is comparatively open, and the sharp edge is very conspicuous already on the inner whorls, as in the gradumbilicate forms of *Ptychites.* The spiral striation seems to be confined to the periphery.

The *Placites*-like *Hyattites* Mojsisovics, 1902*a* (genotype : *Pinacoceras praefloridum* Mojsisovics, 1873) differs from the other discoidal genera here discussed in its suture-line. This has saddles with phylloid terminations, similar to those of *Sturia* and *Procladiscites* but the description of the suture-line of *Hyattites* is not satisfactory. It is not clear, for example, why Mojsisovics called the high external saddle an adventitious saddle, unless in 1873 he interpreted the elements of the suture-line no more precisely than he did the genus *Pinacoceras* itself. He made no correction, however, in 1902(*a*), when creating *Hyattites,* and Gemmellaro (1904) just called it the siphonal saddle.

It may be agreed that the massive median saddle in the external lobe indicates affinity of *Hyattites* with *Sturia,* but if the suture-line happened to be invisible, the discoidal shape of the involute genotype would suggest comparison with *Placites* rather than *Sturia.* On the other hand, such Anisian-Ladinian ammonites as "*Meekoceras*" *maturum* and "*M.*" *emmrichi* Mojsisovics, also included in *Hyattites,* resemble *Sturia* more than the Carnian genotype. They were, however, included in the genus *Beyrichites* by Phillipi already in 1901. There is, indeed, striking similarity between "*Meeko ceras*" *emmrichi* and *Beyrichites proximus* (Oppel), as figured by Diener (1895*b*), except in the much more advanced suture-line of the former, which in its regularity does foreshadow the *praefloridus* type of suture-line.

"*Meekoceras*" *emmrichi* is of Ladinian age and may therefore be looked upon as a development parallel with *Sturia,* but so different from the Carnian *Hyattites* as to deserve a separate generic name. I am suggesting the new name, **Parasturia** gen. nov. (genotype : *Meekoceras emmrichi* Mojsisovics, 1882, p. 219, pl. l, fig. 4). It has the wide external lobe of the *Ptychitidae,* but the saddles are not pyramidal, as in *Sturia,* and the phylloid saddle-endings are rather finely divided. Whether the inner whorls are 'globose' enough to justify inclusion in *Ptychitidae* has yet to be shown. In any case, they are not here expected to be a morphic representation of some Palaeozoic goniatite ancestor in J. P. Smith's sense; and since the Ptychitidae have already been stated to be probably developments of the Meekoceratid root-stock, the occurrence of *Beyrichites*-like transitions is not surprising. For *Sturia* and *Hyattites* have both been linked with the Gymnitidae which are derivatives of the same stock. *Proteusites*, a Ceratitid which may be occasionally indistinguishable from *Ptychites*, is another offshoot of the same root.

B. Family ISCULITIDAE nov.

The separation of the few genera here discussed in a distinct family is suggested partly by the increase in the number of groups now elevated to generic rank, but mainly by their obviously independent status, in spite of the resemblance of their inner whorls to those of the Arcestida. These true Isculitidae, it seems to me, are quite unrelated to the Haloritid forms described above (p. 113) as *Episculites*, *Euisculites* and *Hypisculites*. Some of these Upper Triassic forms had been referred to Arcestidae by Gemmellaro (1904), who dealt in the same paper with numerous trachyostracous ammonites of the family Haloritidae. Since these so-called *Isculites* had been attached to that family by Mojsisovics and his successors, it is difficult to see why Gemmellaro did not also accept their classification, but he did not comment on it. On the other hand, *Smithoceras*, a true Anisian Isculitid, was also taken to include a supposed Arcestid, i.e. an Indian species first described by Diener (1895*b*) as "nov. gen. ind., ex aff. *Arcestidarum*." The suture-line of this form is almost megaphyllitic, but Diener had no hesitation in including it in his genus *Smithoceras*, even if he did not feel justified in giving it a specific name (*S. herminae*) until eighteen years later. The complex suture-line of the type of *Smithoceras* Diener (1907), however, i.e. *S. drummondi* Diener (1907), is rather different, and resembles that of *Juvavites*. Diener, in fact, stated that in spite of its resemblance to the smooth inner whorls of large *Ptychites*, *Smithoceras* was probably the primitive ancestor of the more highly specialized types of *Juvavites* in the Upper Triassic deposits.

Now, it does not seem to me probable that the Anisian

Smithoceras and its close ally *Isculites* are the forerunners of the Haloritids, dominant at a much later period. And since they are not derivatives of the Arcestidae, in spite of their globose, *Arcestes*-like inner whorls, connection with the universal Ptychitidae, rather than the specialized Proteusitidae, is provisionally suggested. It may be mentioned that J. P. Smith (1932) already included *Smithoceras* in the Ptychitidae, but the connection is probably not very close, as already stated, although both may have had a common ancestor among the Paranannitidae.

An important connecting link is the Anisian *Isculites middlemissi* Diener, which has the external aspect of a *Proarcestes*. The small size of what that author called the principal lateral lobe, as compared with the second, seemed to him one of the most remarkable features of the suture-line of that species. Now, this is exactly what is shown in the suture-line of the Anisian "*Sphaerites*" *globulus* Arthaber; and it is probable that the first lobe in these forms is merely an enlarged incision in the external saddle, on the *Didymites* pattern. It seems improbable that this incision corresponds to the wide external lobe in *Ptychites*, with the large and deep second lobe representing the principal lateral lobe, and the small outer saddle the equivalent of that semi-adventitious saddle which arises from the median saddle in so many *Ptychites*. The depth of the external lobe in both *Isculites middlemissi* and in "*Sphaerites*" is against this second assumption. The suture-line of the former, moreover, might be considered to be transitional to the suture-lines of *Smithoceras drummondi* and *S. herminae* on the one hand, and to *Isculites hauerinus* on the other, in all of which the resemblance to the *Ptychites* suture-line is slight and the inequalities in the two lobes reduced or effaced. They are not the suture-lines of an anagenetic Tropitid stock.

Unfortunately, the forms here discussed are very rare and unrepresented in the Collection. It is thus impossible to check their affinities by a study of the development of the suture-line or by thin sections revealing the inner structure. But three sections of *Isculitoides originis* (Arthaber) were made since the appearance of Part IV, partly because it was hoped that they would throw light on the relations with the true Isculitids and, perhaps, of *Thanamites*. They were only moderately successful, however, like most of the sections of the other Paranannitids discussed in this volume, and while they show (collectively) a comparatively small protoconch, a thick siphuncle (25 per cent. of the whorl-height), very convex septa, and long siphonal funnels at first, but shorter ones later (all directed backwards, to the last septum, at 17 mm. diameter), the sections indicate no more than that the reference to the Paranannitidae was correct. In *Proptychitoides decipiens* Spath the protoconch is equally small (if elliptical, through deformation) but the increase in whorl-height is more rapid so that the septa are finally biconvex ; the siphuncle is only one-sixth of the whorl-height in the third whorl ; and the funnels are directed forwards already then (diameter = 4 mm.).

The genus *Isculites* was first briefly mentioned by Mojsisovics in 1886, with *I. hauerinus* (Stoliczka) as its only species. This, therefore, became *ipso facto* the type of the genus. In 1893 Mojsisovics described in detail a group of forms which he erroneously considered to be *Isculites*, but which he correctly attached to the Haloritidae, especially *Anatomites*. Without realizing that he was speaking of two entirely different groups, Mojsisovics then stated that *Isculites*, in Europe, was confined to the Carnian and Norian stages, but that it appeared already in the Middle Triassic in India. Diener, in his ‘ Catalogue ’ (1915), thus unhesitatingly took *Amm. decrescens* Hauer (1855*a*), Mojsisovics's first and presumably most eligible species, as the genotype of *Isculites*.

This was only the beginning of a series of misunderstandings, which it may take some time to straighten out. The confusion was enhanced by Diener's creation of a new genus, *Spitisculites* (1916*e*), for *Clydonites hauerinus* Stoliczka. This, of course, was only a *lapsus*, and the new name has not yet been generally introduced into geological literature, but, as has already been seen, that Anisian species must remain the genotype of the true *Isculites*.

Then Arthaber, in 1911 used *Isculites* for a group of Lower Triassic forms (now *Isculitoides*, see Part IV, p. 197) which are not believed to have any connection with either the Middle Triassic true *Isculites* or the Upper Triassic forms of the group of *Amm. decrescens* Hauer, taken as typical by Mojsisovics and Diener, and by the writer in 1934 (p. 197). The difficulty is that uncoiling body-chambers are found in many unrelated stocks. The Haloritid developments, above mentioned, differ considerably in suture-line from the true Anisian *Isculites*, and the same applies to the Eo-Triassic

Isculitoides, which has already been stated to be more closely connected with the other Parananitidae. As mentioned above, in *Isculitoides originis* (Arthaber) the low whorls, polygyral coiling and the strong convexity of the septa confirm its systematic position. The whorl-height is only 20 per cent. of the diameter (25 mm.) in all three sections. Though the outline of the inner whorls (and the constrictions) are preserved in two slides, the septa are partly missing, except at the end (at 17 mm. diameter) where the short siphonal funnels can be seen to be still directed backwards. In another section there are only 10 septa at 20 mm. diameter. The thick siphuncle is external when seen, but it is hidden on the innermost whorls.

A new name, **Ptychosphaerites** nom. nov. is required for the genus *Sphaerites* Arthaber (1896*b*, *non* Duftschmid, 1805, *nec* Quenstedt, 1852), created for the unique *S. globulus* Arthaber (1896*b* p. 107, pl. x, fig. 5), which resembles the hypothetical "*Nannites*" of the theorist, or a young *Arcestes* in form, but is distinguished by its suture-line. This is comparable to the suture-line of *Isculites*, as already mentioned, and not to the *Ptychites* suture-line, with the largest lobe, apparently the first lateral lobe, separated from the external lobe by an adventitious element. The similar suture-line of *Isculites middlemissi*, already cited, is much more complex, the saddles are longer and slenderer, but the general plan is the same.

? Genus THANAMITES Diener (1908).

It is well known that ammonites with contracting body-chambers are often catagenetic, and this is apparently true for some of the Lower, Middle, and Upper Triassic forms with excentric last volutions that have in the past been referred to the heterogeneous group "*Isculites.*" The Anisian-Ladinian true *Isculites* are probably not considerably reduced, suturally, and in the case of *Ptychosphaerites* it is possible that the entire saddles are original, not simplified through degeneration. The typical Episculitinae of the Carnian and Norian have reduced Haloritid suture-lines, and they are thus quite independent of the Lower Triassic *Isculitoides*, referred to the ancestral family Paranannitidae in Part IV. There is, however, yet another group of Ladinian "*Isculites,*" characterized by entire saddles and a bifid principal lobe, apart from a globose shape. They constitute the genus *Thanamites* Diener, 1890 (genotype : *T. bicuspidatus* Diener, 1908*a*) of Ladinian age, which also covers the Timor " *Isculites* " *ladinus* Welter (1915), with a similar suture-line. The presence of an extra saddle in the suture-line of another Timor species, *T. bihatiensis* (Welter) is probably not of systematic importance, at least by itself ; but it is to be noted that this second Timor species also lacks the protuberance in the first lateral lobe, and thus is not a typical *Thanamites*. It may be a suturally reduced *Isculites* and will serve as a warning not to overrate the importance of the differences in the suture-line of its companion species, *Thanamites ladinus*. The Peace River " *Isculites* " *schooleri* McLearn (1930) may be a comparable form, judging by the brief description of its suture-line as much simpler than in typical *Isculites* of similar form. An actual example of this British Columbian species in the Collection (No. C. 39723) does not show a suture-line on the globose inner whorls, and the outer whorl is occupied by the contracting body-chamber. The Himalayan *Thanamites bannensis* Diener, again, with an extremely depressed whorl-section, like that of the inner volutions of *Didymites*, is a typical species.

The length of the body-chamber in *Thanamites* is one whole whorl or over, which is not very helpful. In *Ptychites* it is about three-quarters to just over one whorl ; in *Lobites* and *Isculites* it is one and a half. *Thanamites* may resemble Arcestids in general appearance, whorl-shape, and smoothness, but not in its simple suture-line. In Arcestida, as in the Phylloceratida, the suture-line never became reduced to anything like the same extent. The suture-line of *Thanamites* is under-developed as regards the number of elements, and, as Diener stated, it is the suture-line of the Trachyostraca, so that he included the genus in the Tropitoidea. The linking of *Thanamites*, in Broili's revision of Zittel's ' Grundzüge,' with the Tropitid genus *Styrites* is thus not inapt. The young *Tropites subbullatus* (Hauer) also has a bifid lateral lobe (see Hyatt & Smith, 1905, pl. lxxix, fig. 2) though, comparing this figure with the development of the suture-line of the same unmistakable species in Branco (1879, pl. v, fig. ii), doubt is again raised immediately as to the value for classificatory purposes, of such small differences.

Thanamites is thus now attached to the Isculitidae, though with some doubt, and, like them, is believed to have originated in the Paranannitidae, as presumably did the Ptychitidae and the Arcestidae (Part IV, p. 197).

INCERTAE SEDIS.

c. Family NANNITIDAE Diener, 1897, emend.

The genus *Nannites* Mojsisovics, 1881 (genotype: *Goniatites spurius* Münster, 1843) has always lent itself well to phylogenetic speculations on account of its reputed globose shape and very simple suture-line, resembling the Carboniferous goniatites. J. P. Smith, in fact, in Hyatt & Smith (1905), declared that it had been artificially separated from *Glyphioceras* on account of its occurrence in the Trias. This preoccupation with imaginary Carboniferous ancestors, instead of finding nearer relatives, of course, warped J. P. Smith's judgment of ammonites in general. While Hyatt, in 1900, had assigned *Nannites* and *Ptychites* to different superfamilies and different sub-orders, he and Smith, in 1905, in complete disregard of this classification, stated that Mojsisovics and Diener had entirely correctly included *Nannites* in the family Ptychitidae; for the young of all Ptychitids that had been studied by them went through a "*Nannites* stage." This name is wrong; and a similar stage, in any case, could be found in many other groups.

In his latest work, J. P. Smith (1932) assigned the earlier *Nannites dieneri* Hyatt & Smith (1905) to a new genus and to the most unlikely Upper Triassic (and typically Norian) family Haloritidae. He also called it "primitive," i.e. anagenetic, whereas the true *Nannites* of the Middle Triassic (probably meant for the Carnian, i.e. Upper Triassic *N. spurius*) was considered to be "arrested and reversionary," i.e. catagenetic. Arthaber (1914), in calling *Nannites* the most primitive type (of his Ptychitinae), apparently did not envisage its being a catagenetic or degenerate element; for, since he traced the stock back to the Carboniferous *Pronannites* Haug, he probably also accepted the persisting globose stage of his Ptychitinae as anagenetic. Haug, however, already, in 1894, had considered *Nannites* to be out of place in the Ptychitinae, both on account of its suture-line and the goniatitic stage retained to the adult. It is less easy to see why he placed the genus in the Ceratitidae, with prionidian lobes. But it may be recalled that Mojsisovics (1882) had already been baffled by the peculiar characteristics of the genus *Nannites*, which he thought might require a special subfamily. Diener supplied this in 1897(*a*), and both he and Mojsisovics left *Nannites* provisionally in the Ptychitidae, for, as the latter explained, *Ptychites* itself had forms which by their globose shape recalled the Arcestids.

Mojsisovics, however, in 1902(*a*), completely changed his opinion about *Nannites*. He transferred it to the Trachyostraca and the super-family Ceratitoidea, leaving the Ptychitidae in the leiostracous super-family Pinacoceratoidea; but, apart from the statement that this was necessitated by the ceratitic character of the suture-line, the genus *Nannites* was not again discussed. Since no other author, so far as I know, has recently dealt with *Nannites*, and since J. P. Smith's (1932) retention of the genus in Ptychitidae does not so much apply to the true *Nannites spurius* as to a rather hypothetical globose form with a very simple suture-line, it becomes necessary to review the genus.

Unfortunately, there is insufficient material for obtaining additional evidence from the internal structure of *Nannites*. The eleven specimens in the Klipstein Collection, labelled *Goniatites blumi*, include the example figured in pl. viii, fig. 13, and they agree with the form figured as *Clydonites frisei* Münster, by Laube (1869), believed to be the same as *Nannites spurius* (Münster). But one specimen, labelled "*Goniatites friesei* M." (sic) by Klipstein, is more evolute and not a *Nannites* at all, but possibly the nucleus of some form of *Klipsteinia*.

Nannites spurius Münster, then, I take to be well illustrated (natural size and enlarged, but not distinctly marked so) in Laube (1869) and Mojsisovics (1882), the former figuring it as *Clydonites frisei* Münster sp. It will be seen at once that it is not globose. No specimen is known of more than between 5 and 6 mm. diameter, and, since they have their body-chambers (just over half a whorl) and in some cases the ventral rostrum described by Mojsisovics, they are taken to be fully grown. The septate part (3·5 mm.) occupies about 2½ whorls and has 28 septa, as against 2¾ whorls and 36 septa in *Ptychites studeri* or 2⅗ whorls and 37 septa in *Ptychites latifrons* Mojsisovics, as figured in Schindewolf (1934, 1941). The siphuncle is external from the start, and its thickness and the direction of the septa (with the long funnels pointing backwards) are distantly comparable to the corresponding parts in a Palaeozoic type like *Pronorites*, figured by Miller & Unklesbay (1943, pl. i, fig. 3). That genus, however, is probably quite unrelated, and, in any case, has a much larger protoconch. The strong convexity forward of the septa and the direction of the funnels are also reminiscent of the Lower Triassic *Columbites* and *Subcolumbites europaeus* (Arthaber), mentioned on p. 101 ; but this last has a central siphuncle on the inner whorls. Other members of the Parananitidae, namely *Prenkites*, *Arnautoceltites*, and *Prosphingites*[1] proved useless when sectioned, owing to unsuitable preservation. *Paranannites* itself is only slightly better, as mentioned below, and it certainly shows constrictions which are missing in *Nannites*. The pyritic matrix, however, may be responsible for the fact that no constrictions can be seen, except apparently the first. In sections of *Ptychites* these are always conspicuous ; at larger diameters, also, the siphonal funnels point forwards, and there is not even a trace of the backward extension seen on the early whorls.

Since Ceratitids are essentially similar in section, and since the evidence of the internal features is not positive enough for our attempt to classify *Nannites*, we may perhaps resort to the geological horizon and the associated fauna to indicate possible relationships. The fauna of St. Cassian consists of 64 ammonites, as listed by Mojsisovics, with *Nannites spurius*, perhaps significantly, as the last. The list is out of date and there are additional species, some in the Klipstein Collection, listed in the present volume. But these make little difference to the general picture. Apart from the genera with numerous elements in the suture-line, like the Arcestids, *Lobites*, etc., and the evolute *Lecanites*, *Celtites*, etc., there are chiefly the Trachyceratids with comparatively few elements to their suture-lines. These have their own degenerate developments and there are only the "*Dinarites*" (e.g. *Aplococeras eduardi* Mojsisovics sp.) which have a similar goniatitic suture-line. Whether these were likely to produce a more involute and more inflated offshoot, like *Nannites spurius*, it is impossble to say. The allied *Aplococeras avisianum* (Mojsisovics), which occurs in incredible numbers in the Forno Limestone of Ladinian age, is not accompanied by any Nannitid.

The two Ladinian species associated by Mojsisovics with *Nannites spurius* are *N. bittneri* and *N. fugax* Mojsisovics, but they are involute and therefore much more like the supposed goniatitic ancestors of *Nannites*. The first is fully grown at twice the size of *N. spurius* and, in spite of the

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[1] For *Isculitoides* see p. 158.

similarity (but not identity) of the simple suture-line, is almost certainly not a direct forerunner of the evolute genotype. The mut. *asklepii*, doubtfully attached to *N. bittneri* by Renz (1911), is not a *Nannites*, with its deep constrictions on the outer whorl, but possibly some immature Arcestid, as Renz himself suggested. Its suture-line, moreover, is known, and as it is of Carnian age, it certainly has nothing to do with *N. bittneri*. *N. fugax* is larger altogether and, since the unknown body-chamber may have been even more galeate than the nucleus and excentrumbilication may have set in, it is possibly more closely allied to the Isculitinae than to *Nannites spurius*.

Nannites contractus Smith (1914), from the *Daonella* Beds of the Middle Triassic of Nevada, has a similar section but more evolute coiling even than *N. spurius*. If it be a forerunner of the Carnian type, then Mojsisovics may have been right in attaching *Nannites* to the Ceratitida. For there can be no connection between *N. contractus* and the earlier, constricted "*Paranannites*" *oviformis* Smith, with closed umbilicus, a ceratitic suture-line, and the whorl-shape of *Ptychites latifrons*, and therefore neither a *Nannites* nor a *Paranannites*. If it were not for its simple suture-line with few elements, it would be near the presumed root of the Arcestids and Ptychitids.

Paranannites Hyatt & Smith having already been described in Part IV (p. 190) as probably a dwarf offshoot of the Proptychitidae, is not taken to be directly connected with *Nannites*. It differs chiefly in its ceratitic suture-line, also in the longer body-chamber ; but it has an external siphuncle, and the number of septa could be held to correspond (20 to the whorl at 15 mm. ; 15 to the volution before, at 7·5 mm. ; 9 and 7 on the next two inner whorls). But the protoconch and the first whorl were not cut in the median plane so that comparison is difficult.

There only remains *Paraganides* as the last of the genera in the sub-family Nannitinae, as understood by Hyatt & Smith in 1905. This genus is now included in Haloritidae (see p. 111) for it has nothing to do with *Nannites spurius* and is also quite different from *Tornquistites*, another degenerate Tropitid, now interpreted as a reduced Tropiceltitid (p. 95).

I made two sections of *Paraganides* when preparing the sections described in a paper on the "Evolution of the Cephalopoda" (1933*a*, pp. 433, etc.), and these were seen by Böhmers, who referred to them in 1936 (p. 81). *Paraganides* has an open umbilicus in the young but becomes perfectly involute already at a diameter of under 3 mm., with a flattened, Cladiscitid whorl-shape. Its siphuncle is unusually large, as in *Tropites*, and the funnels are exactly the same ; the siphuncle is also internal at first and still a third of the whorl-height away from the venter quite near the end of the septate stage, on the fifth whorl. Even in *Lobites*, in which the siphuncle also never becomes external, this is much nearer the venter throughout. The close septation of *Paraganides* is also quite different from the spacing of the septa in the genera mentioned ; there are 30 septa on the last chambered whorl (at 5–6 mm. diameter) in both sections. Quite unlike *Nannites*, the funnels are short and directed forwards from the third whorl on. There are no constrictions except the first, at about 320°.

Böhmers was impressed by the resemblance of the siphuncular structures of *Paraganides* to those of *Tropites*, and I am also putting the genus into the Tropitida, i.e. the family Haloritidae (see p. 111). But I am relying just as much on the general external resemblance to *Anatomites*, as on the internal features. Van Voorthuysen (1940) echoed Böhmers's remarks and thought that *Paraganides* had to be included in the Tropitida ; he probably altogether over-rated the systematic importance of the internal features of ammonites. In the case of *Nannites* they are not decisive or even helpful, so that the genus is doubtfully left in the family Ptychitidae. But, like *Didymites* and *Lobites*, the genus *Nannites* really occupies an isolated position.

XI. Super-family PINACOCERATIDA Mojsisovics, 1896

Mojsisovics's revision of this super-family in 1902(*a*) left in it the families Pinacoceratidae, Gymnitidae and Ptychitidae, among others ; and, although the first two seemed connected by intermediaries, I have always considered the Ptychitidae to be as distinct as, for example, the Megaphyllitidae, also attached to this super-family by Mojsisovics. In the genealogical table published by Hyatt & Smith (1905), however, the three families above mentioned were widely separated, although Hyatt had previously (1900) united Ptychitidae and Gymnitidae in one super-family.

Haug's alternative scheme of 1907 seemed more attractive on the whole. He also assumed the existence of different goniatitic radicles, but he at least grouped the Ptychitidae with Arcestids and Cladiscitids, whereas the Pinacoceratidae and Gymnitidae were taken to be descendants of another stock. In 1913 J. P. Smith stated that Gymnitidae were commonly regarded as a sub-family under the Ptychitidae, which was true of Arthaber's classification (1911) ; but Smith thought that Gymnitidae were more probably an offshoot from the Lecanitinae. This last sub-family (of the Meekoceratidae) included, besides *Lecanites* itself and *Badiotites*, some Permian and Lower Triassic genera which have nothing at all to do with the Lecanitidae, as here understood (p. 63). Most of the "*Lecanites*" of geological literature are degenerate forms (in the case of the true *Lecanites*, of a Trachyceratid stock), and they are as unlikely roots of the discoidal stocks as *Nannites* is of the globose groups, or as the equally degenerate *Cymbites* was (in Buckman) for a host of Liassic families.

Smith's later scheme (1927*a*) still showed the groups now included in the present super-family as traceable to different goniatite ancestors, but, in his final account (1932), Smith also accepted the origin of Pinacoceratidae in Gymnitidae, as previously agreed on by Mojsisovics, Diener and Arthaber.

Meanwhile, Diener's most recent classification (1925) not only excluded *Sturia* from the Gymnitidae (with which family they had been grouped by Mojsisovics), but he seemed to separate them widely from Pinacoceratidae. This, however, may have been accidental. Only a few years previously Diener (1915*a*, 1919) had shown that *Pinacoceras* and *Placites* independently originated in *Gymnites*, and that the Sageceratidae, placed next to the Pinacoceratidae (in 1925), had a fundamentally different mode of formation of the adventitious lobes and saddles.

The grouping of *Gymnites* and *Ptychites* in Hemiostraca (in Kutassy, 1933), as opposed to Trachyostraca and Leiostraca, does not seem to be helpful ; these terms have no longer any systematic significance, any more than Macrodoma, Metriodoma and Microdoma.

Without getting back, then, to Mojsisovics's classification, it is proposed to include the two families under discussion in one super-family Pinacoceratida. I stated repeatedly, in Part IV, that the Pinacoceratidae were intimately connected with the Gymnitidae, from which they were derived ; and the transfer of *Placites*, a direct successor of *Gymnites*, to the Gymnitidae (in Diener) from the original Pinacoceratidae (Mojsisovics and Arthaber) is of little import. But, for some time, I was at a loss to separate the Gymnitidae from the Ptychitidae. The placing of *Sturia* alone (Ptychitidae in Diener and Arthaber, Gymnitidae in Mojsisovics) seemed to show that they could not be widely different.

A. Family PINACOCERATIDAE Mojsisovics, 1896.

The genus *Pinacoceras* Mojsisovics, 1873 (genotype: *P. metternichi* Hauer sp., 1846*a*) includes the typical group of *P. metternichi* and *P. parma*, which is widely known as representing the acme of ammonite specialization, at least in so far as subdivision of the septal edge is concerned. The evolute *imperator* group had not been separated from the involute *parma* group, until Arthaber (1927) created the sub-genus *Parapinacoceras* for *Pinacoceras subimperator* Mojsisovics (1873), previously known only by its suture-line. Only, since the name *Parapinacoceras* has already been employed by Diener (1916*e*), the new name, **Eupinacoceras** nom. nov. (genotype: *Pinacoceras subimperator* Mojsisovics, 1873, p. 64, pl. xxvi, fig. 5) will have to be used instead. I would provisionally include in it also *P. imperator* (Hauer), for, although, according to Mojsisovics, the venter of Hauer's original (refigured in 1902*a*) is acute, not truncate, the figure published by Arthaber shows a restored, bicarinate venter which is considered a special feature of *P. subimperator*. The preservation of these very slender, evolute forms, unfortunately, is always defective, and it remains to be seen whether *Eupinacoceras* will have to be restricted to only one species among the evolute forms of *Pinacoceras*.

It is as yet uncertain whether another new group of *Pinacoceras* is indicated by *P.* nov. sp. ind. of Diener (1919, p. 44, text-fig. 17), which has feeble tubercles on the sides, reminiscent of those of *Gangadharites* (see Part IV, p. 425).

Parapinacoceras Diener, 1916*e* (genotype: *Pinacoceras aspidoides* Diener, 1900*b*) was established for the Anisian forms which are contemporaries of *Gymnites* and still have the comparatively simple suture-line of the latter genus, but the closed umbilicus and oxynote shape of the true *Pinacoceras*. There is, of course, also resemblance to *Placites*, especially in forms like *Parapinacoceras subclausum* (Hauer), or the variety figured by Salopek (1911), in which the periphery is still somewhat rounded and not yet sharpened to an acute edge.

Pompeckjites Mojsisovics, 1902*a* (genotype: *Ammonites layeri* Hauer, 1847) was separated from *Pinacoceras* on purely external features, and the suture-line differs only slightly, chiefly in not showing the convexity so clearly, since the auxiliary series is slightly ascending towards the umbilicus. Diener (1915*b*) figured two consecutive suture-lines of a young example which show the rapid increase in the number of adventitious elements by the breaking up of the external saddle.

Bambanagites Mojsisovics, 1896*a* (genotype: *B. schlagintweiti* Mojsisovics, 1896), confined to the Norian of the Himalayas, has *Pompeckjites*-like ornamentation, at least on the earlier whorls, but a simpler suture-line with sub-phylloid saddle-endings. Diener (1906*a*) thought that his *B. kraffti*, from the *Tropites* Limestone of Byans, differed from the typical species described by Mojsisovics only in the development of an acute siphonal edge, after an early *Pompeckjites*-stage, but the differences in the suture-lines are also striking, in my opinion. The irregularly frilled saddles of *B. kraffti* are reminiscent of those of degenerate Meekoceratids of the Lower Trias.

The genus *Protoplatytes* Cockerell (1905) was introduced, in place of *Platytes* Mojsisovics, 1902*a* (preoccupied), for *Pinacoceras neglectus* Mojsisovics, 1873, which has a comparatively open umbilicus and a simple Gymnitid suture-line. Since it comes from the uppermost Norian, however, it cannot be a *Gymnites*, as its author thought in 1882. Nor is it likely to be a Tropitid (Mojsisovics, 1902*a*), in view of its suture-line and the shape of the umbilicus which, even in a crushed *Discotropites*, would look entirely different.

The genus *Placites* Mojsisovics, 1896*a* (genotype: *Pinacoceras platyphyllum* Mojsisovics, 1873) is easily distinguished from *Pinacoceras* by its flat sides and rounded venter, combined with a closed umbilicus. Its suture-line is simple, as in *Gymnites*, and finely divided, with the outer branch of the external saddle becoming individualized, to form an adventitious saddle. Those forms in which it does not do so have been separated as *Paragymnites* Hyatt, 1900 (genotype: *Placites sakuntala* Mojsisovics, 1896*a*), but this genus has been considered unnecessary by Diener. It may be mentioned that Hyatt & Smith (1905), when describing another species of *Paragymnites*, did not even mention the existence of this genus, but the difference between the suture-lines of *P. humboldtensis* (Hyatt & Smith) on the one hand, and *Placites polydactylus* (Mojsisovics) on the other, is not less than that between many another pair of closely allied genera, established by Hyatt.

Pinacoplacites Diener, 1916*e* (genotype: *Placites meridianus* Welter, 1914) was created (as a sub-genus) for a form which Diener, in 1915(*b*), described as extraordinarily striking. For it combined with a distinct opening-out of the umbilicus a development of the adventitious elements which otherwise was met with only in *Pinacoceras*. The genus *Paraplacites* Kutassy (1928*b*) and its genotype: *P. nopcsai* Kutassy (1928*b*) are both *nomina nuda*, and should never have been allowed to appear in print.

The genus *Placites* was studied in thin sections by van Voorthuysen (1940), and he showed that its siphuncle, external from the start, was much thinner than it is in Tropitid genera. In Arcestidae and Cladiscitidae, with a somewhat similar siphuncle, the size of the protoconch and other features differed, so that it was considered more probable that *Placites* belonged to an independent "group." There are many other Upper Triassic ammonites with which *Placites* does not agree, and since v. Voorthuysen mentioned that Arthaber (1927) had called *Placites* as of "uncertain systematic position," it may be recalled that this view meant precisely that *Placites* showed affinities with both *Gymnites* and *Pinacoceras*. The chapter on the phylogenetic position of *Placites* by v. Voorthuysen, thus, was not a notable advance on what previous authors had deduced from purely external considerations.

As *Placites* had been included in Pinacoceratidae (Mojsisovics) and Gymnitidae (Diener) it was advisable to compare its microscopic characters with sections of at least *Pinacoceras* and *Gymnites*, not to mention distant genera like the rare *Tibetites*, which, according to Hyatt, had the same mode of generation of its adventitious elements as *Placites*. This, van Voorthuysen failed to do, but, unfortunately, there is lack of suitable material to fill this gap in our knowledge. The few Pinacoceratids available for sectioning (one *P. damesi* Mojsisovics, and two *Pompeckjites layeri* Hauer sp.), owing to their extreme thinness, proved difficult, so that the sections are not median and it is uncertain whether the siphuncle was external from the start, as in *Placites* or *Gymnites*. The septa seem very closely spaced in *Pinacoceras* on account of the rapid increase in whorl-height; actually, there are as many as 35 at 18 mm. diameter, and 23 on the next inner whorl (8·5 mm.). *Pinacoceras*, thus, has not only the most elaborate suture-line of all ammonites, but has them more closely spaced than any other, though the Upper Cretaceous *Gaudryceras*, with its extremely polygyral whorls, exceeds it in actual number of septa. In *Pompeckjites* the spacing is at least as close as in *Pinacoceras* at an equal size (42 at 25 mm. diameter), but one section has only 10 septa on the first whorl at ·66 mm. diameter, following on a small protoconch (·3 mm.).

B. Family GYMNITIDAE Waagen, 1895, emend.

This family is now kept apart from Ptychitidae, as already mentioned, for, in spite of the existence of forms like *Ptychites gymnitiformis* Hauer, described as a "real" transition between the two genera, the resemblance is superficial. The family is, however, closely allied to Pinacoceratidae (Part IV, p. 8) and even to Monophyllitidae, by way of the ornamented *Leiophyllites*, wrongly included in *Xenaspis* by Welter (1915). The true *Xenaspis* Waagen is of Permian age, and *Flemingites* of the Lower Trias, also included in this family by Waagen, has already been dealt with as one of the Meekoceratida (Part IV, p. 107). This leaves only *Gymnites* itself in the family, and Waagen did not discuss it, since it does not occur in the Salt Range. But it is worth while recalling the fact that Waagen considered Hauer's *Ceratites crasseplicatus* and *C. striatus* to be forms of *Flemingites*. This partly explains why the limits between the two families, Ptychitidae and Gymnitidae, have to be constantly readjusted, and it does not support J. P. Smith's (1914) contention that the resemblance is purely external and does not indicate near kinship. Moreover, there is the general agreement in the suture-lines of *Gymnites*, *Discoptychites* and *Sturia*, which last genus also has changed from one family to the other, and perhaps with equal propriety. But J. P. Smith's listing of *Japonites* under both Ptychitidae and Gymnitidae was probably unintentional. In 1932 he had it in neither, but in Ceratitidae.

The genotype of *Gymnites* Mojsisovics (1882) is *Ammonites incultus* Beyrich (1867), selected by Diener ('Catalogue,' 1915). Arthaber, in 1927, categorically pronounced that *G. humboldti* had to be considered the genotype, but he did not attempt to justify this substitution. As now restricted, the genus includes evolute, smooth, discoidal shells with oval whorl-section and arched venters. The suture-line has a wide external lobe, finely divided elements, with the second lateral saddles and the auxiliaries descending steeply to the umbilicus. This typical group is confined to the Anisian, and the shells attain a diameter of up to 200 mm., when they may acquire straight costation.

The *Gymnites* of the Ladinian and Carnian have a narrower umbilicus and are now referred to *Epigymnites* Diener, 1916*e* (genotype: *Gymnites ecki* Mojsisovics, 1882). This often has a row of lateral tubercles, like certain *Sonninia*. When the periphery becomes sharpened or bluntly keeled, the forms are included in *Anagymnites* Hyatt (1900); but the genotype of this, namely *Ammonites lamarcki*[1] Oppel (1863) is characterized by a much more distinct, umbilical slope with a sharp edge, reminiscent of *Malletoptychites*. The suture-line of this small Anisian group is simpler than that of the typical *G. incultus*; the oft-quoted *G. acutus* Hauer, however, with a rounded umbilical edge and a *Japonites*-like suture-line, might not be considered to be a typical *Anagymnites*.

It seems, nevertheless, that Diener was right in including *Gymnites acutus* in *Anagymnites*. The young *A. lamarcki*, at 40 mm. diameter, has proportions: ·42—·30—·30; in a Bosnian example of *A. acutus* (No. C. 40613) at 28 mm. diameter, they are: ·40—·33—·33, and at 15 mm. the whorl-thickness is still 33 per cent. It is possible that this example belongs to the var. *involuta* of Gugenberger (1927), for which he gives, at a much larger diameter (67·5 mm.), the following proportions: ·50—·24—·27. In the similar *Tropigymnites planorbis* (Hauer), at 28 mm. diameter, the proportions are: ·30—·25—·54, but in this particular example (No. C. 20349) the umbilicus is rather large, for Hauer gives the proportions as: ·28—·21—·49 at 60 mm. diameter. The suture-line in the adult, of course, has to be relied on for definite identification,

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[1] The original spelling, adopted in Diener, is *lamarki*, but as the name was given in honour of J. B. de Lamarck, Oppel's spelling was

for in the young *A. acutus*, at 15 mm. diameter, it is comparatively simple, fairly straight, and the septa are distantly spaced. The suture-line, then, is rather different from that of a young *Gymnites*, but already at 28 mm. the dependent auxiliaries appear, the external saddle is narrow-stemmed, and the adult *Japonites*-stage is reached. In *Tropigymnites* there is only one auxiliary lobe and the whole suture-line looks simple and straight. But it is sufficient to compare the suture-line of the similar *T.* ? *chandra* (Diener) and that of *Japonites sugriva* Diener, to see that the differences are rather subtle. A common root might explain the similarity ; and Hyatt already had grouped the Celtitidae and Ceratitidae, with their Meekoceratid ancestors in one of his sub-orders. Gymnitidae may well have to be attached to the same root-stock.

A new name seems indicated for *Gymnites spiniger* Diener 1917*b*, p. 110, text–fig. on p. 111), which is a typical form of the *incultus* group, but which develops ventral spines, followed by paulostome constrictions. I propose for it **Xiphogymnites** gen. nov., as this type of tuberculation is unique in ammonites and entirely against the rules accepted by the followers of Buckman's ornament " cycles." Even pairs of peripheral tubercles, without a previous costate stage, as in *Analytoceras* (*Ammonites hermanni* Gümbel) are not envisaged in any cycle, though they have their corresponding, periodic ridges. Single tubercles, however, developed on the siphonal line in an otherwise perfectly smooth stock are so extraordinary that to future workers *Xiphogymnites* may yet become a classical example of one type of ammonite–specialization. The crested siphonal ridges of *Haidingerites* or of comparable Jurassic types are on a different footing.

Paragymnites Hyatt, referred to Gymnitidae by Arthaber (1914), is discussed above under Pinacoceratidae ; but included in the present family is *Buddhaites* Diener, 1895*b* (genotype : *B. rama* Diener, 1895*b*). This was created for a unique Gymnitid, distinguished from the typical forms by its narrow umbilicus, high and sharpened whorls and a row of peculiar folds in the middle of the flat lateral area. *Gymnites jollyanus* (Oppel), also from the Himalayan Anisian, lacks the sharpened venter, small umbilicus and long series of auxiliaries, but has similar ornamentation. It connects *Buddhaites* with *Epigymnites*.

The genus *Japonites* Mojsisovics, 1893 (genotype : *Ceratites planiplicatus* Mojsisovics, 1888*a*) was established as a sub-genus of *Ceratites*, but raised to independent rank in 1902(*a*). Being established for a large crushed form which does not well show its periphery or the inner whorls, this genus also had various interpretations, and authors referred to it ammonites as distinct, or possibly as near, as *Tropigastrites* (Celtitidae) and *Pseudodanubites* (Ceratitida). The fact that Diener (1895*b*) described as *Gymnites* a form (*G. ugra*) that was transferred to *Japonites* by Mojsisovics, shows that the two genera are very similar and that the latter author did not consider the possible presence of a keel or sharpening of the periphery a generic feature of *Japonites*. Again, the peculiar ornamentation of the type species, with its recurved ribs and umbilical bulges, is not present in many of the species of *Japonites* in geological literature. In fact, there are grave doubts as to the aptness of Diener's (1915*c*) dictum that *Japonites* was one of the most clearly defined groups of the Middle Trias on account of its combination of characters (Ceratitid and Gymnitid) of externally similar types. For Diener himself considered the Nevada "*Sibyllites*" *louderbacki* Hyatt & Smith (1905) to be a typical *Japonites*, ignoring both ornamentation and suture-line and possibly relying on whorl-shape alone.

The Lower Triassic *Japonites sugriva* var. (*non* Diener), figured by Arthaber (1911), with its perhaps not very accurately restored suture-line, unfortunately must be left out of consideration in tracing the relations of the genus. Being smooth, it could have given rise to the costate Anisian genotype, but the suture-line is entirely different. Arthaber himself thought that *Japonites* was a near relative of the widely umbilicated Ptychitids, i.e. the Gymnitinae in his classification, whereas in 1914 he actually identified *Malletoptychites* with *Japonites*. This is scarcely acceptable, unless the periphery of the Japanese holotype of *Japonites* was originally very wide (to accommodate the presumably wide external lobe and its adventitious saddles), in which case the apparent sharpening is due to crushing entirely and is not of generic importance, as in the carinate *Anagymnites*. But the Albanian form cannot be referred to any of the genera from the same deposit, described in Part IV, and, as it stands out as completely distinct on account of its suture-line alone, it requires a new name : **Eogymnites** gen. nov., genotype to be *E.* **decipiens** nom. nov. for *Japonites sugriva* Diener, var. in Arthaber (1911, p. 231, pl. xx, figs. 4*a*–*c*). Its inclusion in the family Gymnitidae must be tentative for the present. In Part IV (p. 383) I called *Japonites* an offshoot of the Gymnitidae, but if *Eogymnites* is correctly interpreted, it is already too highly specialized to be the immediate ancestor of either *Japonites* or *Gymnites.*

This brings us back to the " Xenaspid " or perhaps Dieneroceratid root-stock, among the Meekoceratida, from which not only the Gymnitidae, but the Phylloceratida, the Ceratitida and the Celtitidae have sprung.

The Collection includes examples of *Gymnites* from Alpine and Balkan localities, the latter especially often of gigantic proportions Though not very common, *Gymnites* is still one of the four principal genera in that Bosnian collection already referred to in 1921 (Spath, p. 348), with 278 specimens, ranging next to *Ptychites* (640), *Arcestes s. l.* (591), and *Monophyllites* (314). This collection also includes at least one new species and an example of the rare "*G.*" *subclausus* Hauer, which is a direct transition to *Parapinacoceras aspidoides* (Diener). There are also specimens from Asia Minor, Timor and the Himalayas, including the ammonites figured by Salter (in Salter & Blanford, 1865), chiefly *Gymnites batteni* (Strachey MS.) Salter, pl. xi, fig. 2 (and pl. vi, fig. 3), which differs from *G. kirata* Diener in having an umbilicus of 33 per cent. of the diameter (60 mm.), not 59 per cent. ; *G. planodiscus* (Salter, pl. viii, fig. 5), *G. salteri* Beyrich sp. (pl. vi, figs. 3, 4) and *Buddhaites rama* Diener (Salter's *Ammonites floridus*, pl. vi, fig. 1).

The preparation of median sections of *Gymnites* did not meet with much success, chiefly owing to the poor preservation of the forms from the Middle Triassic of Bosnia and the scarcity of the group elsewhere. As in *Placites* (see fig. 15 in v. Voorthuysen, 1940, p. 65) there are 24 septa at a diameter of 2 mm., corresponding to the first 2½ whorls, at least in *G. occultus* (Beyrich) ; and the width of the siphuncle is about one-sixth of the height in the third whorl. The siphuncle is external where first seen (on the second whorl) and the funnels are directed forwards and long, especially on the outer whorls. The absence of constrictions is noticeable in *G. occultus* (after the first constriction at about 360°) because in *G. incultus* (Beyrich) there are at least nine constrictions to a diameter of 3·5 mm., but not beyond. The unfavourable preservation of the additional sections of *Gymnites* unfortunately prevented further observations.

INCERTAE SEDIS.

Among the groups which have been doubtfully included in the super-family Ceratitida, is the genus *Bukowskites* Diener, 1907 (genotype : *B. colvini* Diener, 1907), which has an ammonitic suture-line. This is not unlike the suture-line of *Japonites* cf. *dieneri* Martelli, figured by Diener in the same work on the Himalayan Muschelkalk ; and if the keel of that form were replaced by a siphonal groove, the resemblance would be even more impressive, if far from complete. Now, according to Salfeld (1921), the formation of a keel or a furrow on the venter of an ammonoid is of secondary importance for systematic purposes ; and they may appear in the most different groups, and at the same or at different times, independently of each other. Actual examples are not so easily found ; it is not impossible that the genera *Distichites* and *Tropites*, referred to on p. 83, are really closely related. The slow evolution of *Psiloceras* into aulacoid and carinate branches is however scarcely comparable, being on a vastly larger scale.

The genus *Bukowskites* is so different from any other Triassic group of ammonites that the creation of a distinct family seems indicated ; yet the single example of *B. colvini* is not well enough preserved to warrant such a step. It may be only a pathological specimen ; and, in any case, it would be just as difficult to find a position in our systematics for the family as for the genus.

In doubtfully attaching *Bukowskites*, then, to the same family as *Japonites*, the resemblance in the suture-line is relied on and not the external shape, which, as Diener pointed out, is more like that of *Ectolcites*. Grooved venters are not common in the Triassic, except in the Trachyceratida, and I can see no resemblance in shape or coiling to any described form. No other relationship, therefore, seems possible for this Anisian genus *Bukowskites*, the stratigraphical position of which does not appear in doubt.

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